2019 Status of the Lake Ontario Lower Trophic Levels[1]

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Significant Findings for Year 2019:

1) Spring total phosphorus (TP) in 2019 was 3.2 µg/L (offshore) and 4.7 µg/L (nearshore), both all-time lows; however, there is no significant time trend in our data series (1995-2019 for nearshore; 2002-2019 for offshore). Apr/May – Oct mean TP concentrations were low at both nearshore and offshore locations (range, 3.7 – 6.5 µg/L). TP and SRP concentrations were not significantly different between nearshore and offshore habitats.
2) Chlorophyll-*a* and Secchi depth values are indicative of oligotrophic conditions in nearshore and offshore habitats. Offshore summer chlorophyll-*a* declined significantly 1995 – 2019. Nearshore chlorophyll-*a* increased 1995 – 2004 and then stabilized 2005 – 2019. In 2019, epilimnetic chlorophyll-*a* averaged between 1.3 and 2.9 µg/L across sites, and Apr/May – Oct concentrations were not significantly different between nearshore and offshore sites. Summer Secchi depth increased significantly in the offshore 1995 – 2019 from ~6 m to ~8 m (20 ft to 26 ft). In the nearshore Secchi depth increased 1995 – 2004 but has remained around 6 m (20 ft) since 1999. Apr/May – Oct Secchi depth ranged from 3.8 m to 9.1 m (12 ft to 30 ft) at individual sites and was significantly higher offshore (7.6 m; 25 ft) than nearshore (5.7 m; 19 ft).
3) In 2019, nearshore summer zooplankton biomass increased to 16.7 mg/m^3 after an all-time low (10.3 mg/m^3) in 2017. Offshore biomass (12.0 mg/m^3) was near the all-time low (8.1 mg/m^3, 2006). Apr/May – Oct epilimnetic zooplankton density and biomass were not different between nearshore and offshore sites. However, zooplankton average size was significantly higher in the offshore (0.72 mm) than the nearshore (0.61 mm).
4) Peak (July) epilimnetic biomass of *Cercopagis* was 2.4 mg/m^3 in the nearshore and 1.4 mg/m^3 in the offshore. Peak (September) epilimnetic biomass of *Bythotrephes* was 2.0 mg/m^3 in the nearshore and 2.9 mg/m^3 in the offshore.
5) Summer nearshore zooplankton density and biomass declined significantly 1995 – 2004 and then remained stable 2005 – 2019. The decline was due mainly to reductions in cyclopoid copepods.
6) Summer epilimnetic daytime offshore zooplankton density decreased significantly 1995 – 2004, but biomass did not. Density and biomass declined significantly 1995 – 2019. Density was 3885/m^3 in 2019, about one-fourth the level observed the previous year. Offshore summer epilimnetic zooplankton biomass in 2019 was 12 mg/m^3—well below the mean from 2005 – 2018 (20 mg/m^3).
7) Most offshore zooplankton biomass was found in the metalimnion in July and early-October, and in the hypolimnion in September. *Limnocalanus* dominated the metalimnion in July while daphnids comprised most of the biomass in October. In September, *Limnocalanus* dominated the hypolimnion.

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[1] Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Introduction

This report presents data on the status of lower trophic levels of the Lake Ontario ecosystem (zooplankton, phytoplankton, nutrients) in 2019 collected by the US Biological Monitoring Program (BMP). Trophic level indicators for 2019 are compared with data collected by this program since 1995 and with similar long-term data from other sources. Production at lower trophic levels determines the lake's ability to support the prey fish upon which both wild and stocked salmonines depend. The maintenance of current alewife (*Alosa pseudoharengus*) production in the offshore of the Great Lakes is uncertain due to declines in lower trophic level parameters and the general correlation found between lower trophic level production and prey fish abundance (Bunnell et al. 2014). A decline in offshore lower trophic level productivity is considered a main cause for the collapse of the alewife population and decline in Chinook salmon (*Oncorhynchus tshawytscha*) fishery in Lake Huron after 2003 by some authors (e.g. Barbiero et al. 2011, Bunnell et al. 2012), although others point at the importance of predation and winter severity as the causative mechanisms (Dunlop and Riley 2013, He et al. 2015) making the most likely cause a combination of these factors (Riley et al. 2008, Kao et al. 2016). The similarities in the development of lower trophic level indicators in lakes Michigan and Huron (Barbiero et al. 2018) and concern of a similar alewife decline in Lake Michigan as in Lake Huron (Bunnell et al. 2018) led to a decision to decrease Chinook salmon stocking rates in Lake Michigan by some states. Despite declines in offshore productivity, high nutrient levels close to shore are contributing to excessive growth of attached algae (e.g., *Cladophora*) at several shoreline and beach areas (Makarewicz and Howell 2012). The connection between nutrient loading and fish production remains an important research topic in the Great Lakes (Stewart et al. 2016).

From 1995-2019 a research program (hereafter referred to as the biomonitoring program, BMP) was conducted in Lake Ontario with the primary objective of evaluating temporal and spatial patterns in a number of ecological indicators: total phosphorus (TP), soluble reactive phosphorus (SRP), chlorophyll *a* (chl-*a*), Secchi depth (SD), and crustacean zooplankton (density, biomass, species composition, and size structure). Samples were collected from late April through October. These ecological indicators are assessed from spring through fall based on indicator-specific seasonal importance. Springtime (Apr-May) represents a time of peak nutrient levels in many systems, and these nutrients drive biological activity during the entire year. Therefore, spring TP is an important indicator. The summer stratified period characterizes the peak production period for phytoplankton and many zooplankton species; therefore, summer (Jul-Aug) chl-*a* and summer zooplankton biomass were chosen as indicators. The Sep-Oct period is useful to track species such as *Bythotrephes* whose biomass typically peaks later in the year. The BMP is a collaborative project that, in 2019, included the New York State Department of Environmental Conservation (NYSDEC) Lake Ontario Unit and Regions 6, 7, and 8 at Watertown, Cortland, and Avon (Lake Ontario regions); the U.S. Fish & Wildlife Service Lower Great Lakes Fish and Wildlife Conservation Office (USFWS); the U.S. Geological Survey–Lake Ontario Biological Station (USGS); and Cornell University.

In the "State of Lake Ontario" in 2014, Rudstam et al. (2017) summarized data from various sources including the BMP and analyzed trends through 2013. Total phosphorus and chlorophyll-*a* declined and Secchi depth increased from 1980-1995 but all remained stable thereafter. However, Dove and Chapra (2015) reported a continued decline in spring TP into the 2000s based on data from Environment & Climate Change Canada's Surveillance program. Therefore, we are especially interested in any evidence of further decreases in lower trophic level indicators as we incorporate the 2014 to 2019 years in our trend analyses in both the nearshore and offshore areas of the lake. Zooplankton populations have been more variable, likely due to the interplay between vertebrate and invertebrate predators, invasive benthic mussels, increased water clarity, lower epilimnetic production, and increased deep chlorophyll layers (Rudstam et al. 2015, Barbiero et al. 2014, 2019).

Report Objectives

Using data from 1995 to 2019, the following questions were addressed:

1. What is the status of Lake Ontario's lower trophic levels in 2019, and what differences exist between nearshore and offshore sites this year?
2. How does the year 2019 compare to the same indicators in 1995-2018 (using BMP data and other long-term data)?
3. What is the status of the two, non-native predatory cladocerans, *Bythotrephes* and *Cercopagis*?
4. Are there changes in zooplankton community structure (biomass, size, species composition) that could be indicative of changes in alewife or invertebrate predation, or lake productivity?
5. Is the vertical distribution of zooplankton groups changing, possibly a result of more phytoplankton production in deeper water?

Methods

Sampling

Total phosphorus (TP), soluble reactive phosphorus (SRP), chl-*a*, Secchi depth (SD), and zooplankton density, size, and biomass by species were measured at offshore and nearshore sites in Lake Ontario (Figure 1). Samples were collected from seven nearshore sites biweekly from May through October 2019 (12 potential sampling weeks). Inclement weather precluded sampling during one week at Sodus (SOL), and four weeks at Sandy Pond (SPL). Offshore samples were collected during April, July, and September by the R/V Seth Green, and in April, July, August, September, and October by the R/V Kaho. In addition, one station was sampled at night in May by the R/V Seth Green. Nearshore sites had depths ranging from 9.3 to 15.2 m (31 to 50 ft), and offshore sites ranged from 16 to 208 m (52 to 682 ft). The August R/V Kaho samples are for zooplankton only and are from 4 depths (15 m, 30 m, 50 m, and 100 m) on a transect off Oswego, NY; the 15 m depth was included with nearshore samples while the other depths were considered offshore. Nearshore sampling totaled 82 samples taken from eight sites. Offshore sampling totaled 28 daytime samples taken from ten sites and one nighttime sample.

Water Chemistry

Water samples were collected for analysis of chl-*a*, TP, and SRP. Each sample was obtained by using an integrated water sampler (1.9 cm [3/4 inch] inside diameter Nalgene tubing) lowered to a depth of 10 m (33 ft) or bottom minus 1 m (3 ft) where site depth was 10 m or less. The tube was then closed off at the surface end and the column of water transferred to 2 L Nalgene containers. From each sample, a 100 mL unfiltered aliquot was frozen for later analysis of TP (APHA 1998; SM 4500-P). Two liters of water were filtered through a Whatman 934-AH glass fiber filter that was frozen for later analysis of chl-*a* using acetone extraction followed by fluorometry (EPA 2013). A 100 mL aliquot of filtered water was frozen for later analysis of SRP (APHA 1998 SM 4500-P). TP and SRP samples were analyzed at the Upstate Freshwater Institute (UFI). Chl-*a* was analyzed at the Cornell Biological Field Station (CBFS) using a calibrated Turner 10-AU benchtop fluorometer and the EPA standard operating procedure SOP LG 405 (Revision 9, March 2013). Approximately 2 L (0.52 gallons) of water was filtered for each chl-*a* sample.

Quality Control and Variability

To measure analytical precision at nearshore sites, replicate samples for TP and SRP were analyzed. In July, six aliquots of water were taken from the same sample at the seven nearshore sites. Triplicate samples were taken once in August at nearshore sites to determine within-site variability of TP, SRP, and chl-*a*. From each of the three samples, one aliquot was taken for TP, one for SRP, and one for chl-*a* analysis. At offshore locations, duplicate samples for TP, SRP, and chl-*a* were collected throughout the year. Mean values from those duplicates were used in the analyses.

Zooplankton

Zooplankton samples were collected with standard 0.5 m (1.6 ft) diameter, 153-µm mesh, nylon nets equipped with calibrated flowmeters. At nearshore sites, tow depths ranged 9-11 m (30-36 ft). At offshore sites, epilimnetic tow depths ranged 4-24 m (13-79 ft; from the thermocline when stratification was present). At offshore sites less than 75 m (246 ft) bottom depth (four daytime sites), a total water column sample (from 2 m above the bottom to the surface) was collected in addition to the epilimnetic sample when stratification was present. At sites greater than 75 m (246 ft) bottom depth (three daytime sites), one metalimnetic tow (50 m [164 ft] to the surface) and one hypolimnetic tow (90-100 m [295-328 ft] to the surface) were obtained in addition to the standard epilimnetic sample. Zooplankton were anesthetized with antacid tablets and then preserved in the field with 95% ethanol to obtain a final concentration of 70%. At nearshore sites, single samples were collected on a biweekly basis from May to October from 1–2 m (3-7 ft) above the bottom to the surface, depending on weather conditions.

In the laboratory, each sample was strained through a 1.02 mm (0.04 inch) mesh cup to separate *Cercopagis* and *Bythotrephes* from other zooplankton. This was done because *Cercopagis* and *Bythotrephes* form clumps in the sample, making the usual random sub-sampling of 1 mL samples impossible. For each sample that contained clumps of *Cercopagis* or *Bythotrephes*, two analyses were performed - one on the smaller zooplankton and one on the larger zooplankton (including *Cercopagis* and *Bythotrephes*) that were caught in the 1.02 mm mesh strainer. At least 100 larger zooplankton (or the whole sample) were measured and enumerated by sub-sampling organisms from a gridded, numbered Petri dish in which the sample had been homogeneously distributed. In some cases, different subsamples were used for *Bythotrephes* and *Cercopagis*. To calculate the total number of animals in the clumped part of the sample, a ratio of wet weights of the sub-sample to wet weights of the total sample was used.

For smaller-sized zooplankton (i.e., those not retained by the 1.02 mm mesh strainer), at least 100 organisms were counted and measured from one or more 1 mL sub-samples. The sub-sample was examined through a compound microscope at 10-40X magnification. Images from the sample were projected onto a digitizing tablet that was interfaced with a computer. Zooplankton were measured on the digitizing tablet and identified to species (with the exception of nauplii and small copepodites) using Pennak (1978) and Balcer et al. (1984). In earlier years of this project an electronic touch screen (1995-1997) and a 20X microprojector (1998-2000) were used for measuring the zooplankton (Hambright and Fridman 1994). Length:dry-weight regression equations (CBFS standard set, Watkins et al. 2011) were then used to estimate zooplankton biomass.

Data Analyses

April/May to October mean TP, SRP, chl-*a*, SD, zooplankton density, size, and biomass, and zooplankton group biomass between the nearshore sites and the offshore epilimnion were compared by first obtaining monthly means for each site and then fitting a general linear model with month and habitat as categorical predictor variables. Data for zooplankton density, biomass, and group biomass were log10-transformed prior to analysis. Offshore data collected in late April was analyzed with May nearshore data because of the proximity of nearshore to offshore sampling dates for those months. Data from June and August were omitted from this analysis because the offshore was not sampled during those months. Zooplankton were divided into the following six groups: daphnids (*Daphnia mendotae*, *D. pulicaria*, *D. retrocurva*, *D. longiremis*, *D. schodleri*); bosminids (*Bosmina longirostris*, *Eubosmina coregoni*); calanoid copepods (*Leptodiaptomus minutus*, *Skistodiaptomus oregonensis*, *Leptodiaptomus sicilis*, *Leptodiaptomus ashlandi*, *Epischura lacustris*, *Eurytemora affinis*); cyclopoid copepods (*Acanthocyclops vernalis*, *Diacyclops thomasi*, *Mesocyclops edax*, *Tropocyclops prasinus*); other cladocera (*Alona sp.*, *Ceriodaphnia quadrangula*, *Chydorus sphaericus*, *Diaphanosoma sp.*, *Polyphemus pediculus*, *Leptodora kindtii*, *Camptocercus sp*., *Scapholeberis sp.*, *Ilyocryptus sp.*); and nauplii. Four species were analyzed separately from the groups. Those species are: *Bythotrephes longimanus*; *Cercopagis pengoi*, *Holopedium gibberum,* and *Limnocalanus macrurus.* Differences were considered significant at $p<0.05$.

Change point analyses (Taylor Enterprises, Inc. 2003) were performed separately on nearshore and offshore data to test for breaks in the data. Analyses were performed on spring TP, Apr/May – Oct SRP, summer chl-*a*, summer epilimnetic zooplankton density and biomass, and zooplankton group biomass. SRP data were available for 1998 – 2019 in both habitats. Offshore TP data were available for 2001 – 2019. Change point analysis uses cumulative deviations from the mean to detect changes in time trends and to estimate when those changes occurred. This is done by resampling the data series 1000 times to construct confidence intervals based on the inherent variability in the data series, and testing if and when the observed data series differ significantly from these confidence intervals. Regression analyses for time trends (JMP Pro v12.0.1, SAS Institute Inc. 2015) were performed on three time stanzas (1995 – 2019, 1994 – 2004, and 2005 – 2019) for the offshore and nearshore using spring TP, summer chl-*a*, summer epilimnetic zooplankton density and biomass, and zooplankton group biomass. Zooplankton group biomass could not be normalized and Spearman rank correlation was used on those data. Nighttime zooplankton data are not included in time trend analyses. Zooplankton migrate up in the water column at night causing an increase in density and biomass in the epilimnion; therefore, results from day and night are not comparable.

Results

Quality Control and Variability

To estimate analytical precision (i.e. within sample variability), 42 TP and 42 SRP samples (7 sites x 6 samples per site) were analyzed. Coefficients of variation (CV=SD/mean) ranged from 6 to 37% (mean of 22%) for TP and from 0 to 47% (mean of 20%) for SRP. Values from replicated sampling occasions were averaged for all analyses. Variation for SRP is smaller because many samples had concentrations below the detection limit of 0.6 µg/L. In those cases, the sample was assigned the detection limit. Variability was similar to previous years.

The analysis of August nearshore TP, SRP, and chl-*a* triplicate samples showed that the CV for TP ranged from 16 to 58% (mean of 29%), the CV for SRP ranged from 0 to 44% (mean of 8%), and the CV for chl-*a* ranged from 0 to 6% (mean of 4%). Within site variability for TP was typical of the variation observed in previous years. Variability of SRP was lower than usual because many samples had values below the detection limit (0.6 ug/L); those samples were assigned a value of the detection limit. Note that the variability among replicate samples in the field and variability resulting from laboratory procedures are similar. Values were averaged for later analyses.

2019 Water Quality

May through October mean chl-*a*, TP, SRP, and SD were similar across nearshore sites in 2019 (Table 1). Chl-*a* was lowest at Niagara West Lake (NWL; 1.2 µg/L) and highest at Chaumont Lake (CBL; 2.9 µg/L) (Table 1). TP was highest at Chaumont Lake (CBL; 6.5 µg/L) and lowest at Sodus Lake and Oak Orchard Lake (SOL and OOL; 4.5 µg/L). Chaumont Lake had the highest SRP (1.1 µg/L). SD was lowest at the site Niagara West Lake (NWL; 3.8 m [12 ft]) and highest at Galloo Island Lake (GIL; 7.7 m [25 ft]). Measurements of the same parameters at offshore locations also showed low variability. Chl-*a* ranged from 1.3 µg/L (Mid Lake) – 2.0 µg/L (Oak Orchard-O), TP ranged from 3.7 µg/L (Main Duck) – 5.0 µg/L (Oak Orchard-N and Oak Orchard-O), SRP ranged from 0.7 µg/L (Oak Orchard-O and Tibbetts Point) – 1.1 µg/L (Smoky Point-N), and SD ranged from 6.0 m (20 ft; Smoky Point-O) – 9.1 m (30 ft; Mid Lake) (Table 1). Apr/May – October comparisons of TP, SRP, chl-*a*, and SD showed significant differences between nearshore and offshore locations for TP and SD. TP was higher in the nearshore (5.0 µg/L) than the offshore (4.4 µg/L) and SD was higher in the offshore (7.9 m) than the nearshore (5.7 m).

Seasonal trends were also observed for most variables. Nearshore SD was stable (5–6 m [16-20 ft]) Apr/May to October, while offshore SD was highest (12 m [39 ft]) in Apr/May and lowest (5 m [16 ft]) in October (Figure 2a). Nearshore chl-*a* concentrations were lowest in Apr/May (1.1 µg/L) and ranged from 1.6 – 2.2 µg/L the rest of the season. Offshore concentrations were also lowest in Apr/May (1.0 µg/L) but peaked in September (2.6 µg/L; Figure 3a). Nearshore total phosphorus was stable (4 - 6 µg/L) Apr/May to October while offshore TP was lowest Apr/May and July (3.2 µg/L) and then increased to 5.4 µg/L in September, and then to 6.6 µg/L in October (Figure 4a). SRP concentrations were low (<1.2 µg/L) in both habitats for the entire season (Figure 5a).

Water Quality Trends Since 1995

Comparisons with data collected since 1995 show that 2019 had lower (5.6 m [18 ft]) than average SD in the nearshore and average (7.6 m [25 ft]) SD in the offshore (Figure 2b). Summer chl-*a* concentration in the nearshore was slightly higher (2.1 µg/L) and in the offshore was slightly lower (1.4 µg/L) than the long-term mean of 1.7 µg/L for both habitats (Figure 3b). Spring TP concentrations were at the all-time low in both nearshore and offshore habitats (Figure 4b).

2019 Zooplankton

In 2019, mean Apr/May-Oct zooplankton size was significantly higher at offshore sites (Table 2). Density in the nearshore (8605 ind/m^3) was higher than the offshore (7559 ind/m^3), and biomass was higher offshore (25.0 mg dw/m^3) than nearshore (23.7 mg dw/m^3), but these differences were not significant (Table 2). There were no differences in biomass of zooplankton groups between the nearshore and offshore habitats (Table 2). Offshore zooplankton density and biomass were highest in early-October (Figure 6); this coincided with peak biomass of daphnids and cyclopoids (Figure 7). Nearshore density was highest in late-June and biomass was highest in early-October (Figure 6); this coincided with high numbers of bosminids in June and daphnids and calanoids in October (Figure 7).

In 2019, *Cercopagis* and *Bythotrephes* were detected in samples from both habitats (Figure 7; Table 2). *Cercopagis* was first detected in early-June in the nearshore and in mid-July in the offshore. *Cercopagis* peaked during mid to late-July in the nearshore and in mid-July in the offshore (Figure 7). *Bythotrephes* first appeared in mid-June in the nearshore and in late-July in the offshore. *Bythotrephes* biomass was highest in the nearshore and offshore in late-September (Figure 7). During peak biomass, *Cercopagis* accounted for 10% of the total zooplankton biomass in the offshore and 18% in the nearshore, and *Bythotrephes* accounted for 21% of the offshore biomass and 11% of the nearshore biomass.

Comparison of epi-, meta-, and hypolimnetic daytime zooplankton tows showed that most zooplankton were present in the metalimnion at two of the three deep sites (Smoky Point-O and Oak Orchard-O) and were split evenly between the metalimnion and hypolimnion at the third deep site (Mid Lake) sampled during the July stratified period (Figure 8). Toward the end of the stratified period (September), the biomass was more evenly distributed between the meta- and hypolimnion. As the season progressed into October, the greatest biomass was present once again in the metalimnion. From April-October, the epilimnion accounted for an average of just 12% of the total zooplankton biomass.

The species composition of zooplankton in the epi-, meta-, and hypolimnetic tows also changed seasonally. In the epilimnion, calanoids represented the greatest biomass in July, September, and October. The metalimnion was dominated by *Limnocalanus* in July, and daphnids in October. In September, biomass in the metalimnion was split evenly between cyclopoids, daphnids, and *Limnocalanus.* The hypolimnion was dominated by calanoids in July and by *Limnocalanus* in September and October (Figure 9).

Zooplankton Trends Since 1995

Nearshore summer total zooplankton density and biomass declined significantly 1995 – 2019 (Figure 10; Table 3). These declines were driven by significant declines from 1995 – 2004 after which density and biomass stabilized (Table 3, regression results). Change point analysis showed that a negative break occurred in nearshore total zooplankton density and biomass in 1998 (Figure 10; Table 3). In the offshore, there was a significant decline in summer epilimnetic zooplankton density from 1995 – 2004; biomass declined 1995 – 2019 but no decline was observed in either of the two shorter stanzas (Figure 10; Table 3). Change point analysis indicated a negative break in density in 2005 and a negative break in biomass in 2002 (Table 3).

Several trends were noted in nearshore summer zooplankton group biomass (Figure 11, Table 3). From 1995 – 2019, significant declines occurred in bosminid, cyclopoid, and daphnid biomass. At the same time, biomass of *Bythotrephes*, *Holopedium*, and other cladocerans increased significantly (Table 3). Cyclopoid copepods declined 1995 – 2004 and remained stable thereafter. *Holopedium* and *Cercopagis* biomass increased 1995 – 2004 and remained stable thereafter. In the offshore, bosminid and cyclopoid copepod biomass decreased significantly, *Limnocalanus* biomass decreased marginally, and *Bythotrephes* and *Holopedium* biomass increased significantly 1995 – 2019 (Table 3). *Cercopagis* and *Holopedium* biomass increased and *Limnocalanus* biomass decreased 1995 – 2004 and remained stable thereafter. (Figure 12, Table 3).

Cercopagis and *Bythotrephes* biomasses were low compared to overall zooplankton biomass. Therefore, they were plotted separately to better depict patterns (Figure 13). The nearshore showed a positive change point in *Bythotrephes* biomass in 2006 and a negative change point in 2011 (Table 3). In the offshore, *Bythotrephes* biomass showed no breaks while *Cercopagis* biomass increased in 2000. Change points in the nearshore were also evident in bosminids (negative, 2005), calanoid copepods (positive, 2007; negative 2012), cyclopoid copepods (negative 2005) and *Holopedium* (positive 2003; Table 3). In the offshore, change points occurred in bosminids (negative, 2004) and cyclopoids (negative, 2005; positive, 2013; Table 3).

July daytime whole water column zooplankton biomass ranged from 36 – 60 mg/m^3, 2010 - 2019 (Figure 14) with 2019 having the highest reported biomass of *Limnocalanus* in the data series.

Discussion

Secchi depth, chl-*a*, and TP are indicators of lake trophic status (Carlson 1977). In 2019, average April-October values for all sites ranged from 3.8 to 9.1 m SD, 1.2 to 2.9 µg/L chl-*a*, and 3.7 to 6.5 µg/L TP. These values are similar to other years in this decade and within the range for oligotrophic (low productivity) systems (0.3-3.0 µg/L chl-*a*, 1-10 µg/L TP; Wetzel 2001).

Spring TP is a good predictor of summer phytoplankton production in a range of lake sizes (Dillon and Rigler 1975). Spring TP declined from 20 – 25 µg/L in the 1970s to 3 – 7 µg/L in the 2000s in the offshore and to 5 – 11 µg/L in the nearshore (Figure 4b). These values are consistent with data from the Canadian Surveillance Program (Dove and Chapra 2015) and EPA's lower trophic level assessments in the intensive field years of 2003, 2008, and 2013 (Holeck et al. 2008, 2015; Rudstam et al. 2017). EPA Great Lakes National Program Assessment's (EPA-GLNPO) offshore assessment of spring TP in April at 8 sites ranged between 7.8 and 4.3 µg/L between 1996 and 2019 (GLENDA). Spring TP has been mostly below or only slightly above the goal of 10 µg/L at both offshore and nearshore sites since the BMP started in 1995 (Figure 4b). The all-time low spring TP in 2019 is consistent with the decline in TP reported by Dove and Chapra (2015, data up to 2013), but the 2019 low year did not result in significant time trends since 2002 in our data set. There is a significant downward trend in the EPA-GLNPO spring TP data both between 1996 and 2018 ($p<0.0001$) and between 2002 and 2018 ($p=0.04$).

Summer chl-*a* in 2019 was slightly higher in the nearshore (2.1 µg/L) and lower in the offshore (1.4 µg/L) compared the long-term mean (1995 – 2018) of 1.7 µg/L in both habitats (Figure 3b). Summer chl-*a* decreased significantly in the offshore 1995 – 2019 and increased significantly in the nearshore 1995 – 2004 (Table 3). Despite the absence of trends in chl-*a* in either habitat 2005 – 2019, negative change points were detected in 2009 in both habitats, suggesting a continued decline in recent years. Analysis of satellite data indicate lower surface chlorophyll in 2018 and 2019 than earlier years (EPA-GLNPO 2019, Barry Lesht, unpubl. data).

Mean summer Secchi depth has not changed significantly since 1995 in the nearshore but has increased significantly in the offshore areas (Table 3). Secchi depth increased 1995 – 2004 in both habitats and stabilized thereafter, and no change points were detected in either habitat. An increase since 1985 is also evident in the spring offshore data from GLNPO, although less so for the August data (EPA GLNPO 2019, Rick Barbiero, unpubl. data).

Summer epilimnetic zooplankton density and biomass decreased significantly in the offshore and in the nearshore 1995 – 2019 (Table 3). Biomass declined to below 20 mg/m^3 for the first time in 2002 in the offshore (Figure 12) and in 1999 in the nearshore (Figure 11), declines that have been attributed to increased *Bythotrephes* abundance in the offshore and *Cercopagis* in the nearshore (Warner et al. 2006, Barbiero et al. 2014, Rudstam et al. 2015). These trends are consistent with observed effects of these predatory zooplankton elsewhere (Lehman and Caceres 1993, Yan et al. 2001, Pangle et al. 2007). *Bythotrephes* biomass has been increasing in the offshore since 2015 (Figure 13). During this time, cyclopoids and daphnids have declined.

Generally, *Bythotrephes* abundance is negatively correlated with alewife abundance due to predation (Johannsson and O'Gorman 1991, Barbiero et al. 2014). In our Lake Ontario samples, offshore *Bythotrephes* biomass was low 1995 – 2003 and again in 2014. However, this is not consistent with measures of adult alewife abundance, which was relatively stable from 1997 – 2016 (Weidel et al. 2019). Note that alewife abundance is estimated in spring while *Bythotrephes* peak biomass estimates are from fall (September – October). Therefore, changes that occur over the course of the summer may also contribute to the lack of consistency between alewife abundance and *Bythotrephes* biomass. Nonetheless, these inconsistencies suggest the interaction between alewife and *Bythotrephes* is more complicated than suggested by Barbiero et al. (2014) and Rudstam et al. (2015).

Despite only limited evidence of declining alewife abundance in the trawl surveys (Weidel et al. 2019), there are indications of reduced vertebrate planktivory in Lake Ontario. In an analysis of offshore zooplankton 1997 – 2016, Barbiero et al. (2019) observed the appearance of *Daphnia mendotae* in a daphnid community previously consisting almost exclusively of the smaller *Daphnia retrocurva,* and a shift in dominance in the predatory cladoceran community from *Cercopagis* to *Bythotrephes.* Similar patterns were observed in our offshore data; *Daphnia mendotae* biomass increased significantly 1995 – 2019 while *Daphnia retrocurva* biomass remained stable, and *Bythotrephes* biomass increased 1995 – 2019 while *Cercopagis* biomass remained stable. The presence of larger-bodied zooplankton in both these groups suggests a reduced level of vertebrate planktivory. This is consistent with the alewife abundance model estimate which indicate that 2019 alewife biomass is at an all-time low (Weidel et al. 2020).

The deep chlorophyll layer (Scofield et al. 2017, 2020) and associated zooplankton are not part of the long-term data set collected by the BMP. However, more attention has been focused on this layer since 2010 and whole water column (100 m or bottom minus 2 m to the surface) zooplankton tows are being collected, as does the EPA-GLNPO program. These EPA data show little decline in the offshore zooplankton biomass from 1998 to 2019 (Barbiero et al. 2019, Watkins and Rudstam, unpubl. data), and whole water column data from the BMP (2010 – 2019) support this observation (Figure 14). However, there are community changes, with more cyclopoid copepods in 2013 – 2015 and again in 2018 and more calanoids and daphnids in 2010 – 2012 and 2016; 2017 is an intermediate year with more cyclopoids and fewer calanoids and daphnids than in 2016, but not yet similar to 2014 – 2015. *Limnocalanus* remained a dominant species throughout 2010 – 2019. These results are similar to the offshore whole water column BMP data 2010-2019 (Figure 14).

The BMP data indicate stable lower trophic conditions in Lake Ontario since 2005. This is consistent with the analysis by Rudstam et al. (2017). However, there is some evidence of continued oligotrophication, particularly in the offshore. Spring TP declined in the offshore EPA and Environment Canada Surveillance data sets, and 2019 results revealed spring TP levels at historically low concentrations. Offshore SD increased significantly since 1995 while summer chl-*a*, and epilimnetic zooplankton density and biomass declined. Evidence of oligotrophication in Lake Ontario is strongest prior to 2005, but recent indications suggest it is continuing. However, Lake Ontario is still more productive than lakes Michigan and Huron.

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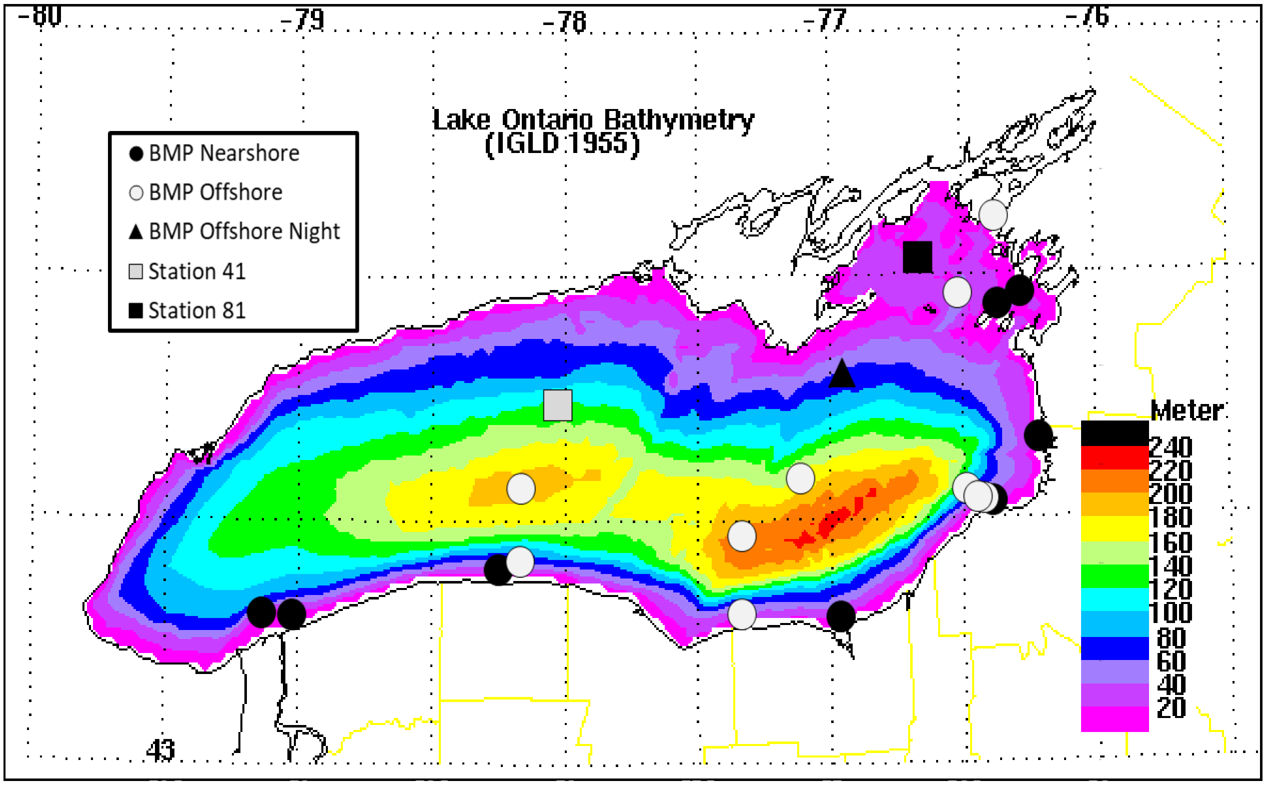


Figure 1. Map of Biomonitoring Program sites, 2019. Station 41 and station 81 are locations sampled by the Department of Fisheries and Oceans Canada's Bioindex Program (1981 – 1995) and are included here as reference for long-term data included in subsequent figures. Offshore stations are deeper than 20 m (66 ft). Nearshore stations are 10-17 m (33-56 ft) deep.

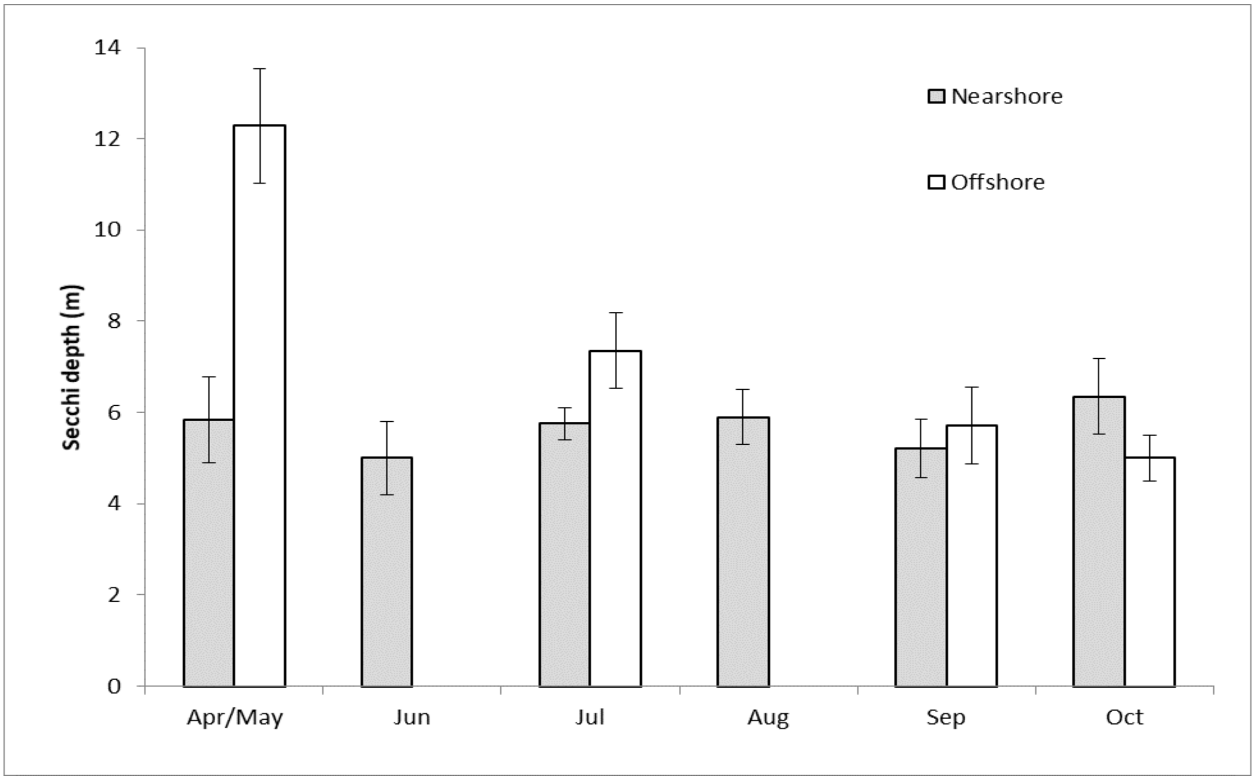


Figure 2a. Mean monthly Secchi depth (meters) for nearshore and offshore habitats in Lake Ontario, Apr/May - October, 2019. Error bars are + *1SE.*

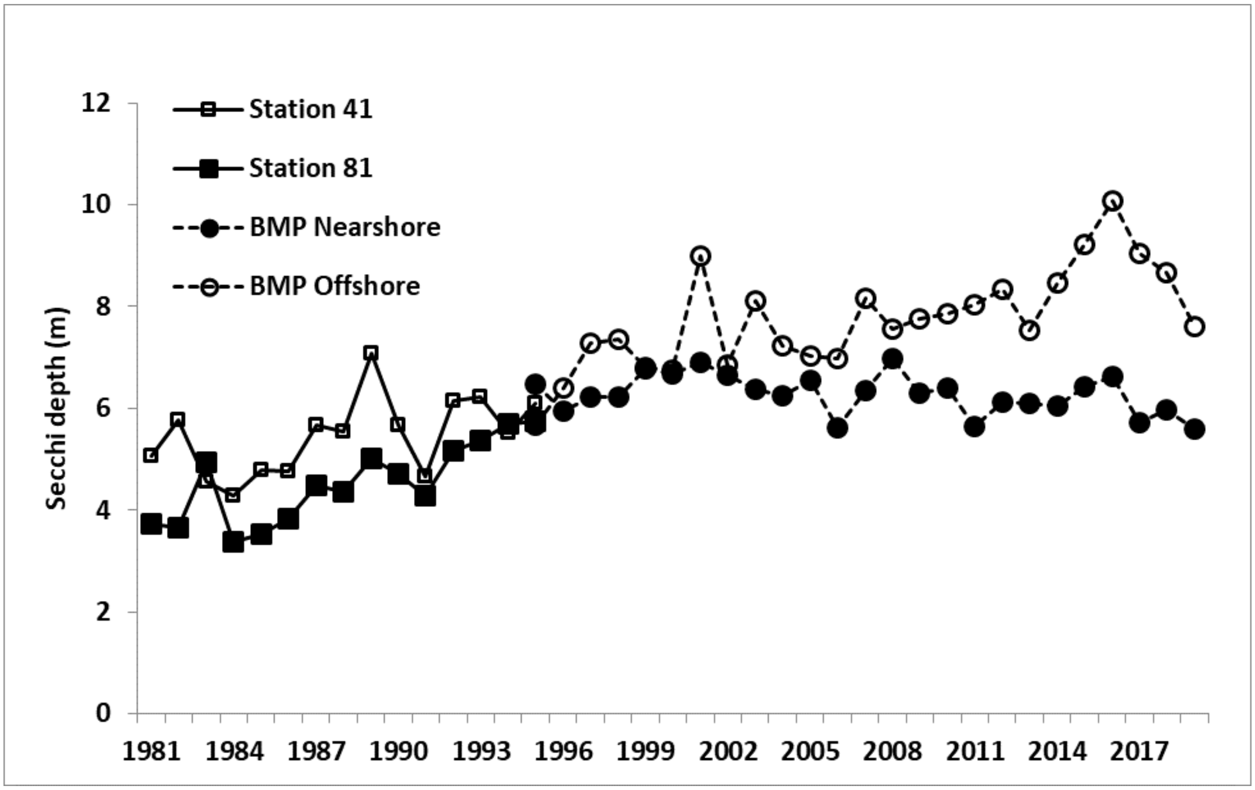


Figure 2b. Long-term mean Apr/May – October Secchi depth (meters) in Lake Ontario, 1981 – 2019. Station 41 and Station 81 are from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 1995 – 2019 are from the US Biomonitoring Program (BMP).

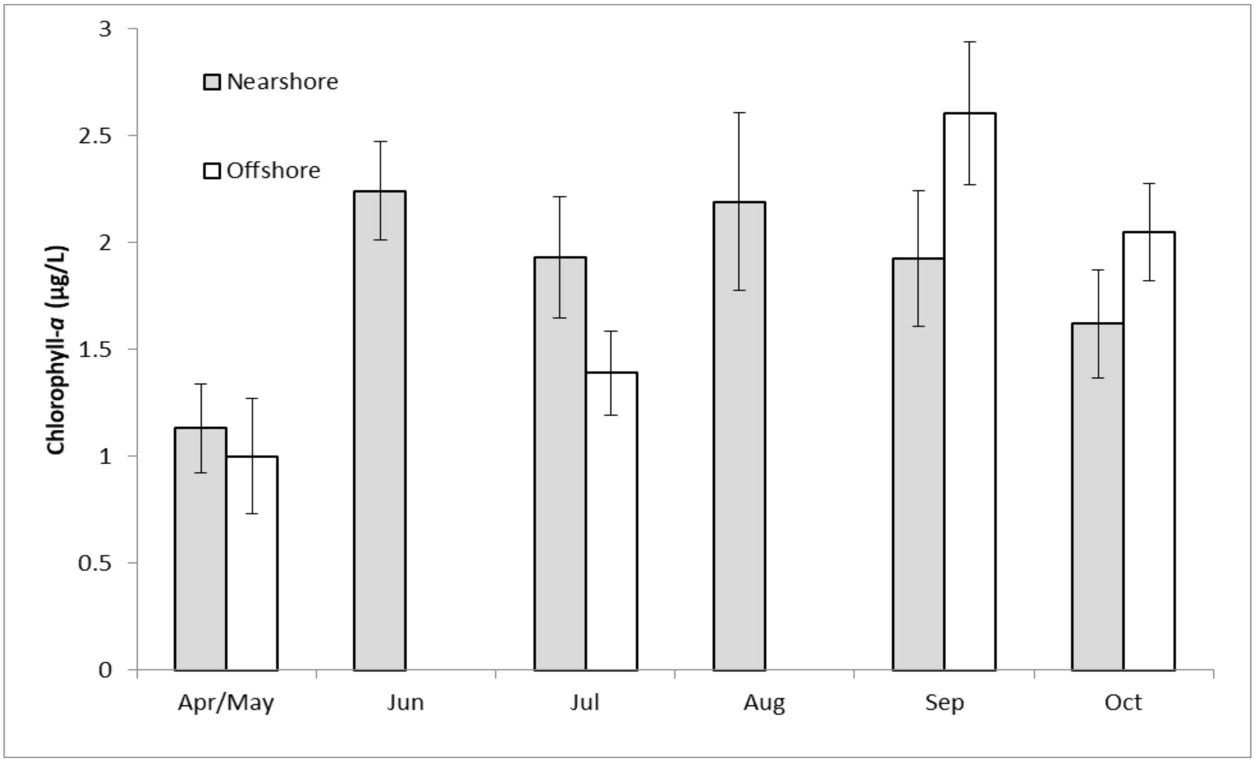


Figure 3a. Mean monthly epilimnetic chlorophyll-a concentrations for nearshore and offshore habitats in Lake Ontario, Apr/ May - October, 2019. Error bars are ± *1SE.*

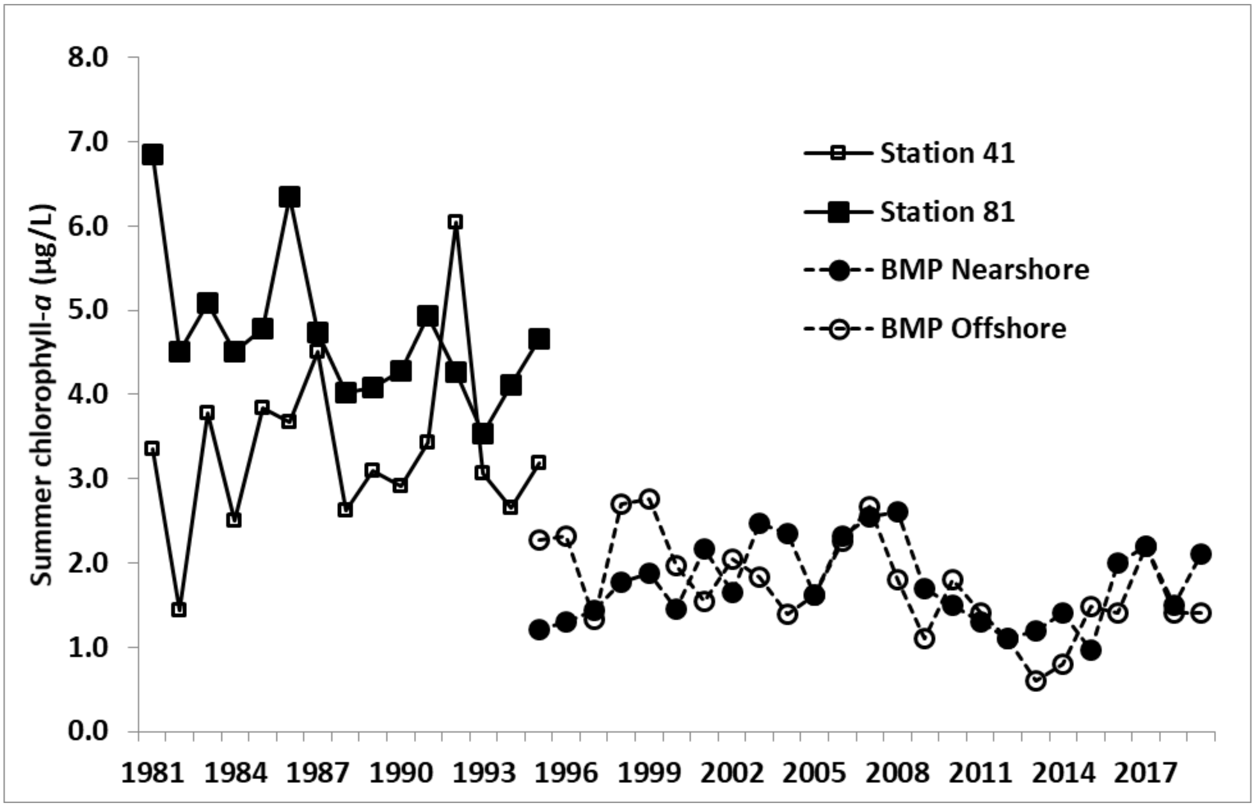


Figure 3b. Long-term summer (Jul – Aug) epilimnetic chlorophyll-a concentrations in Lake Ontario, 1981 - 2019. Station 41 and Station 81 are from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 1995 – 2019 are from the US Biomonitoring Program.

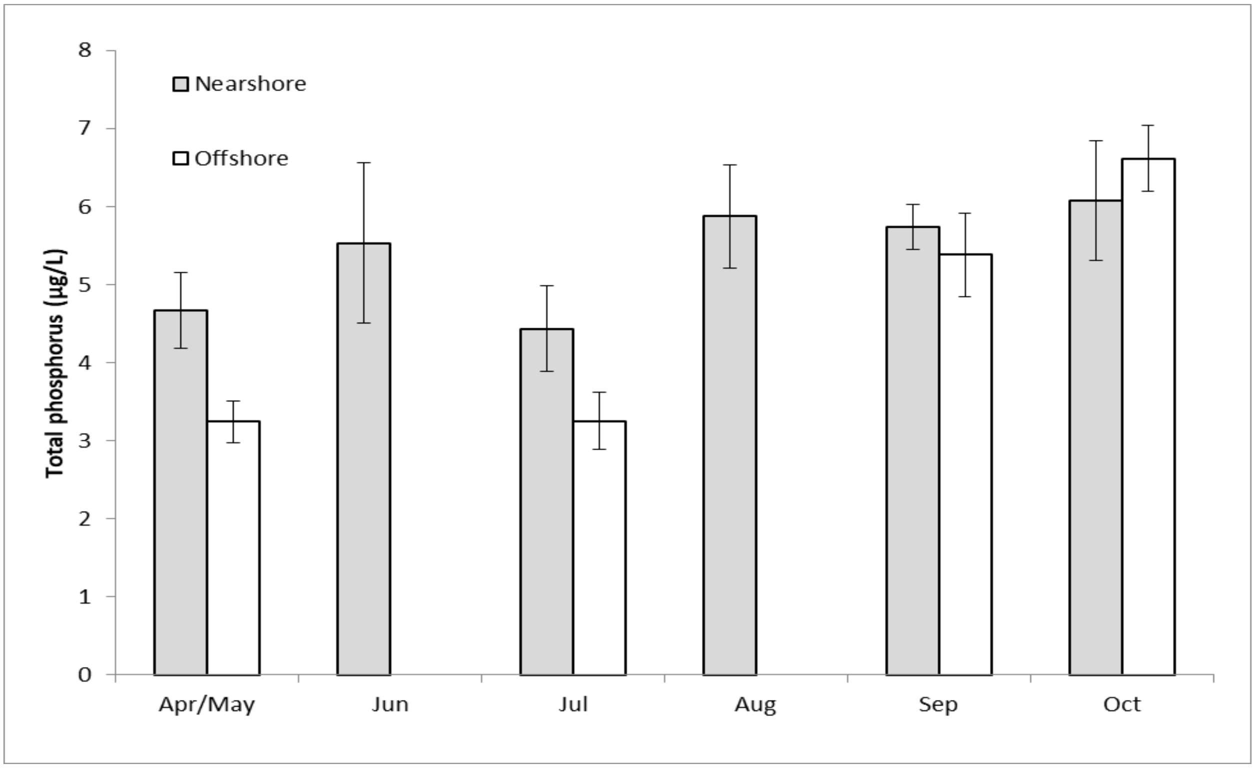


Figure 4a. Mean monthly total phosphorus concentrations for nearshore and offshore habitats in Lake Ontario, Apr/May - October, 2019. Error bars are + 1SE.

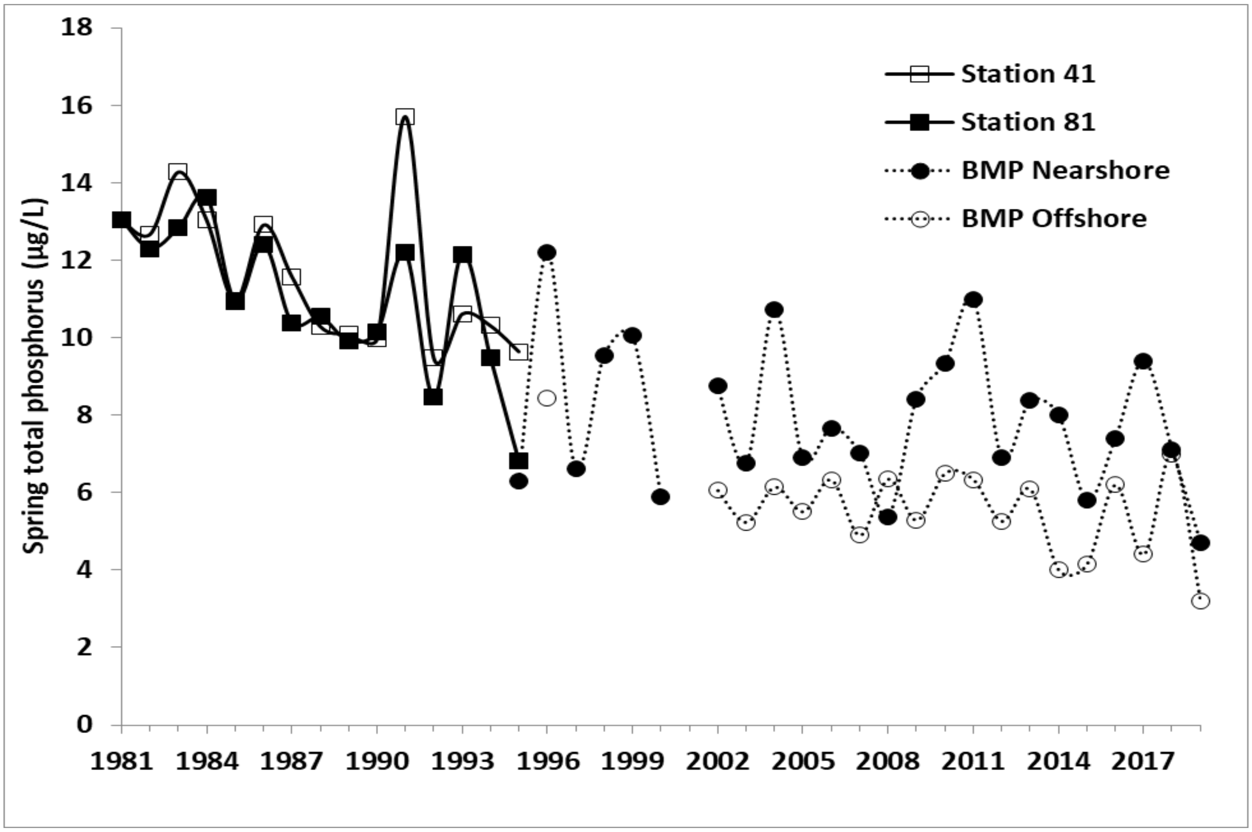


Figure 4b. Long-term spring (Apr – May) epilimnetic total phosphorus concentrations in Lake Ontario, 1981 - 2019. Data from 1981 – 1995 are from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 1995 – 2019 are from the US Biomonitoring Program.

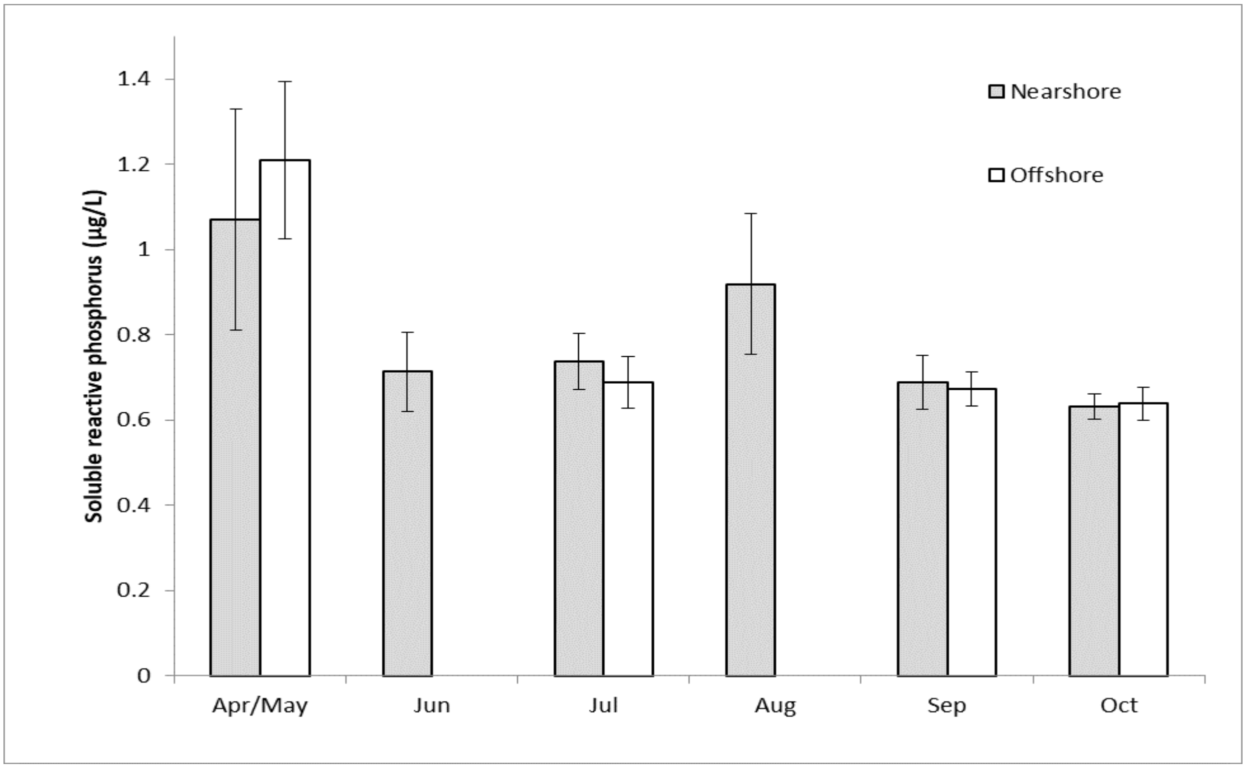


Figure 5a. Mean monthly soluble reactive phosphorus concentrations for nearshore and offshore habitats in Lake Ontario, Apr/May - October, 2019. Error bars are ± 1SE.

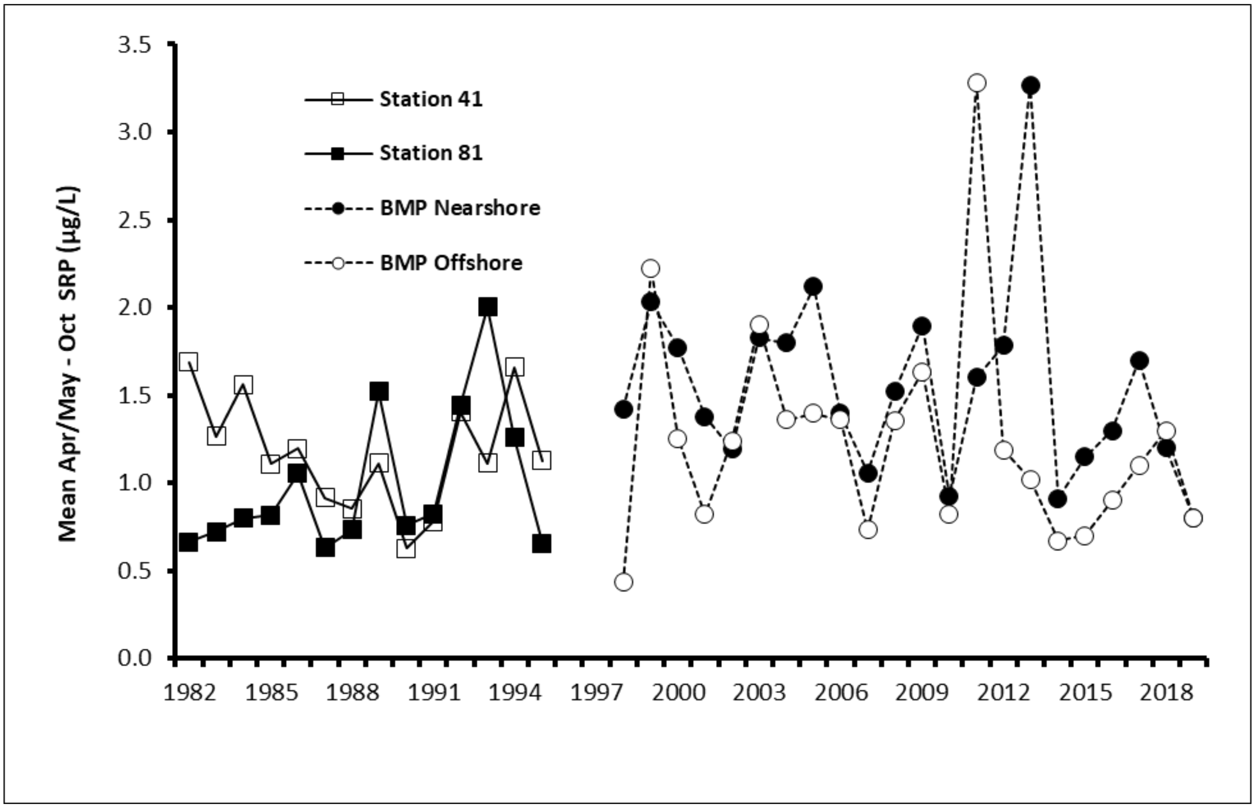


Figure 5b. Long-term mean Apr/May – October soluble reactive phosphorus concentrations in Lake Ontario, 1982 – 2019. Station 41 and Station 81 are from the Department of Fisheries and Oceans Canada's Bioindex Program. Data from 1998 – 2019 are from the US Biomonitoring Program.

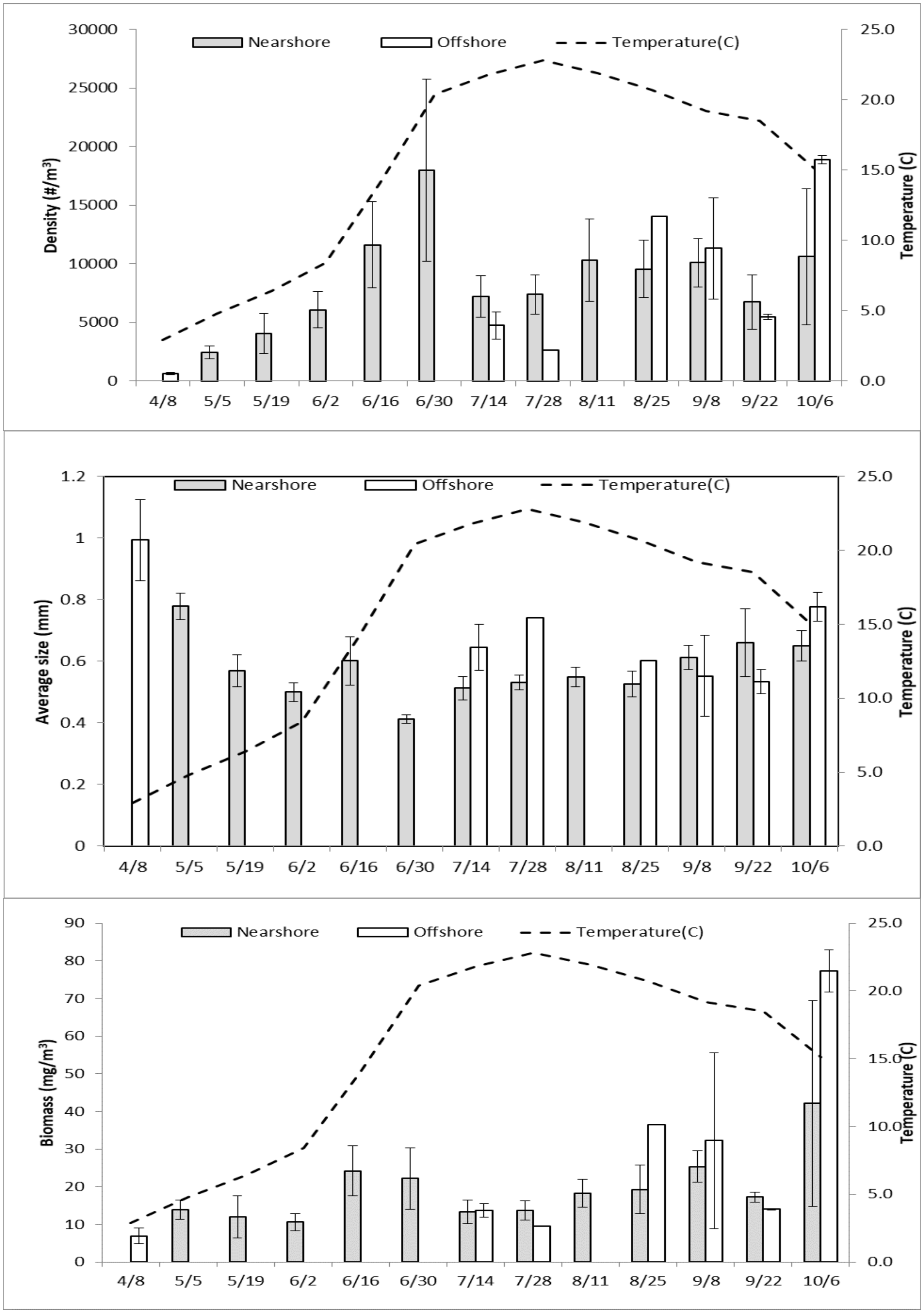


Figure 6. Biweekly mean (± 1 SE) daytime epilimnetic zooplankton density, size, and dry biomass for April through October 2019 at nearshore and offshore sites on Lake Ontario. On the x-axis, biweeks are designated by the date beginning each biweek. When no error bar is present, only one sample was taken that biweek. Lake surface temperatures (secondary y-axis) are from NOAA CoastWatch web site (https://coastwatch.glerl.noaa.gov/ftp/glsea/avgtemps/2019/glsea-temps2019_1024.dat).

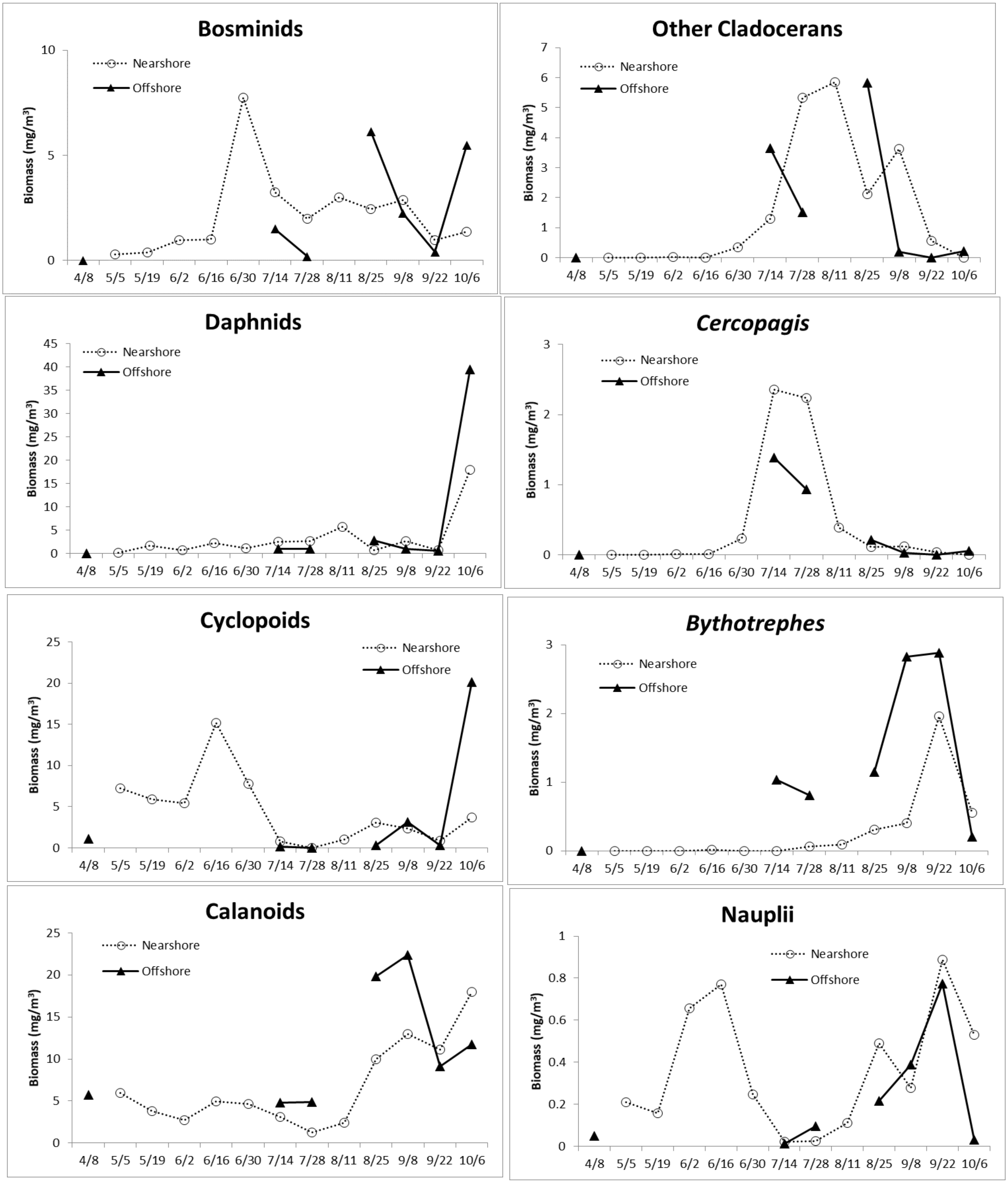


Figure 7. Daytime epilimnetic dry biomass of zooplankton community groups for nearshore and offshore areas of Lake Ontario, April - October 2019. Note different y-axis scales. On the x-axis, biweeks are designated by the date beginning each biweek.

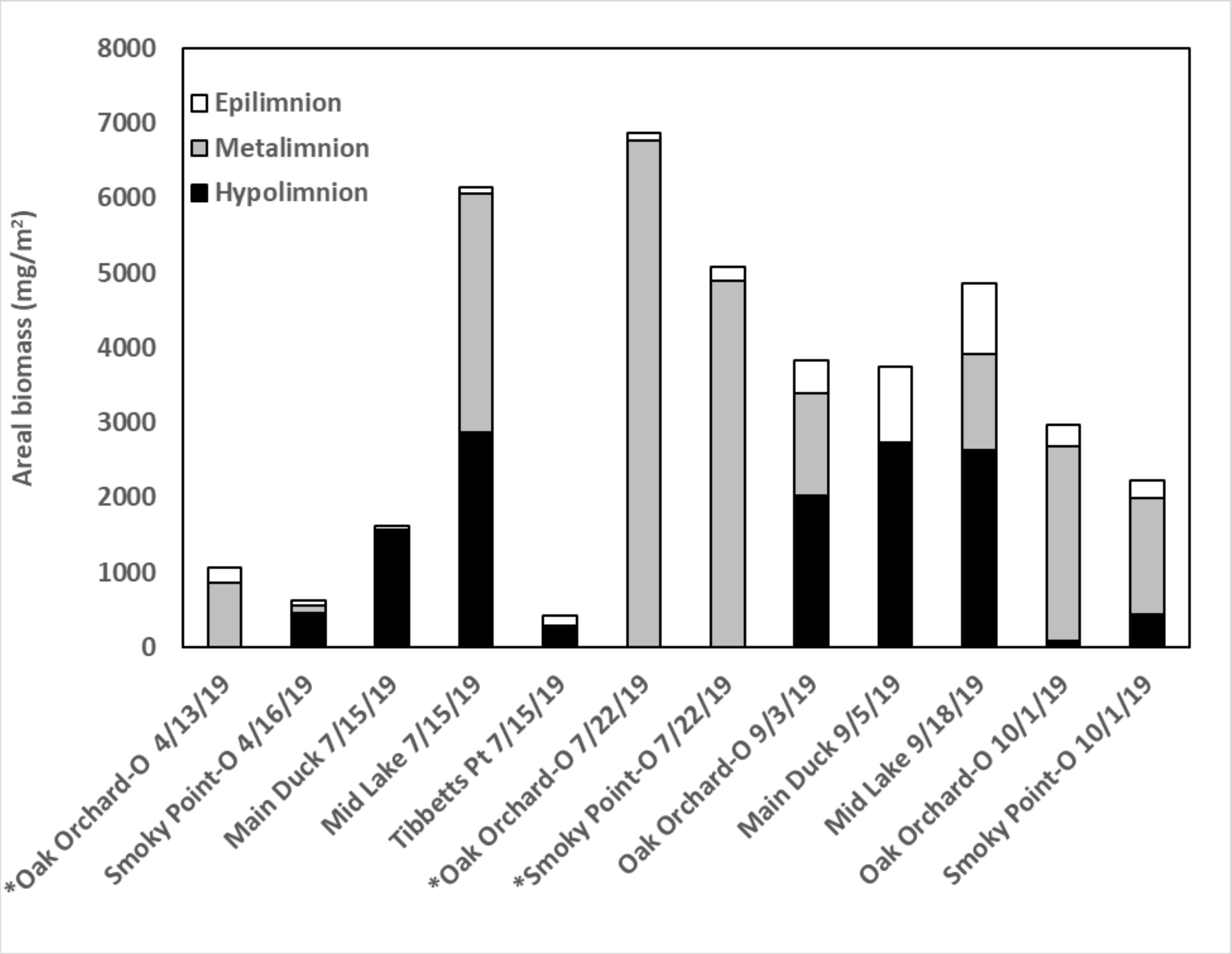


Figure 8. Daytime epilimnetic, metalimnetic, and hypolimnetic zooplankton dry biomass (areal) in Lake Ontario's offshore, 2019. Epilimnetic values determined directly from the epilimnetic tow. Metalimnetic values determined by subtracting epilimnetic tow values from the metalimnetic tow. Hypolimnetic values determined by subtracting metalimnetic tow values from the hypolimnetic tow. Stations without metalimnetic values are shallower stations where only two tows were performed (Main Duck 7/15, Tibbetts Point 7/15, and Main Duck 9/5). A value of zero was assigned when values were negative due to variation in catch of zooplankton between metalimnetic and hypolimnetic tows. Those stations are marked with an asterisk.

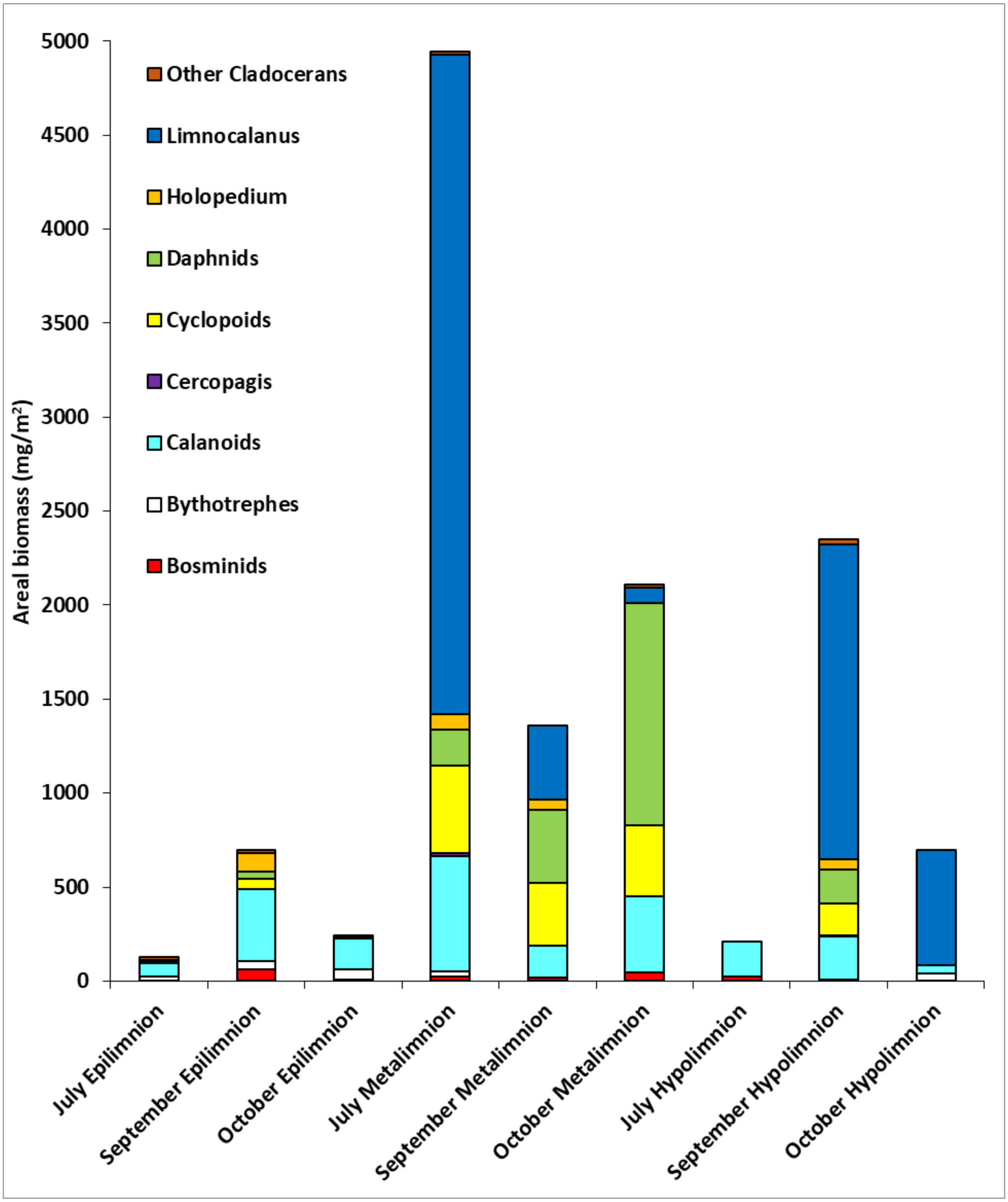
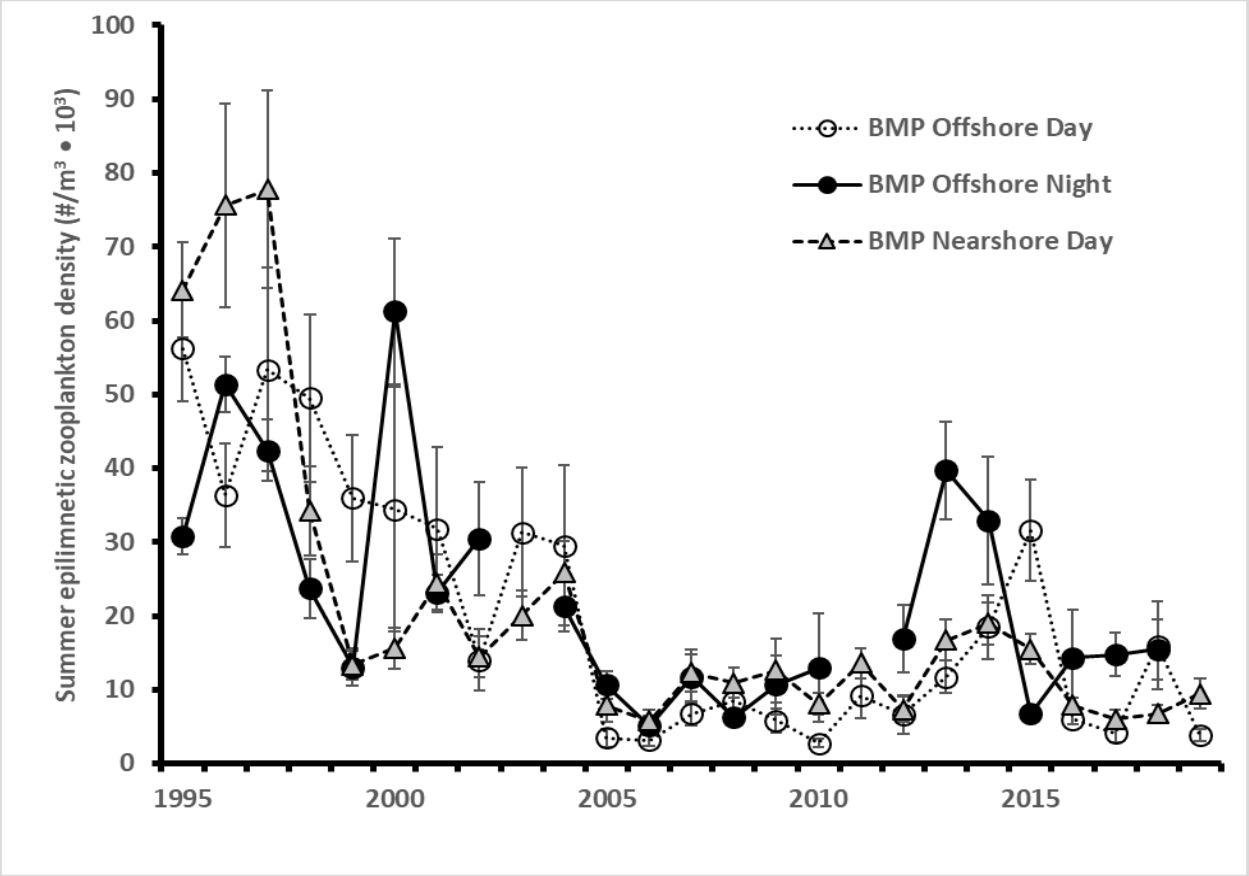


Figure 9. Comparison of mean daytime zooplankton dry biomass in epilimnetic, metalimnetic, and hypolimnetic samples taken from deep (>100m) sites in Lake Ontario's offshore, July, September, and October 2019. The epilimnetic strata includes zooplankton from the top of the metalimnion (4 – 20 m) up to the surface, the metalimnetic strata includes zooplankton from 50 m up to the top of the metalimnion, and the hypolimnetic strata contains zooplankton from 100 m up to the bottom of the metalimnion. A value of zero was assigned when values were negative due to variation in catch of zooplankton between epilimnetic and metalimnetic tows or between metalimnetic and hypolimnetic tows.



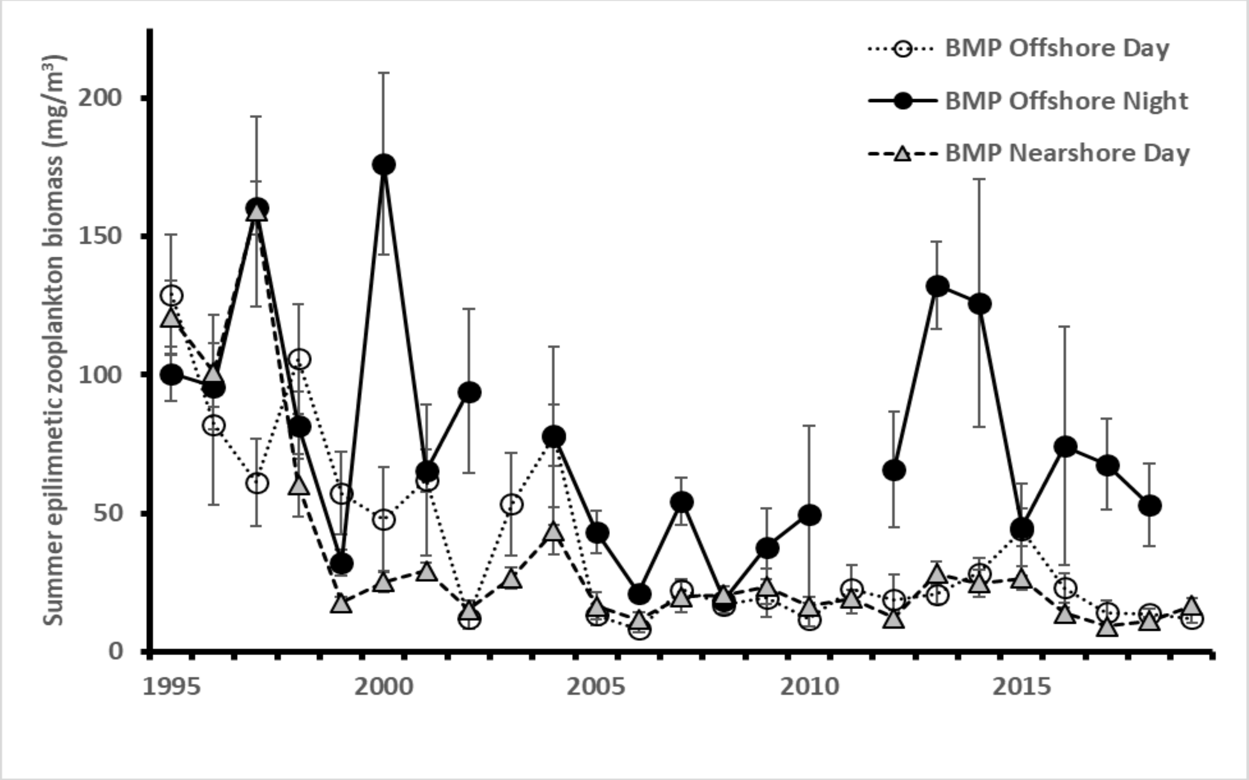


Figure 10. Mean summer (Jul-Aug) epilimnetic zooplankton density (top panel) and dry biomass (bottom panel) in nearshore and offshore habitats in Lake Ontario, 1995 – 2019. Error bars are ± *1 SE.*

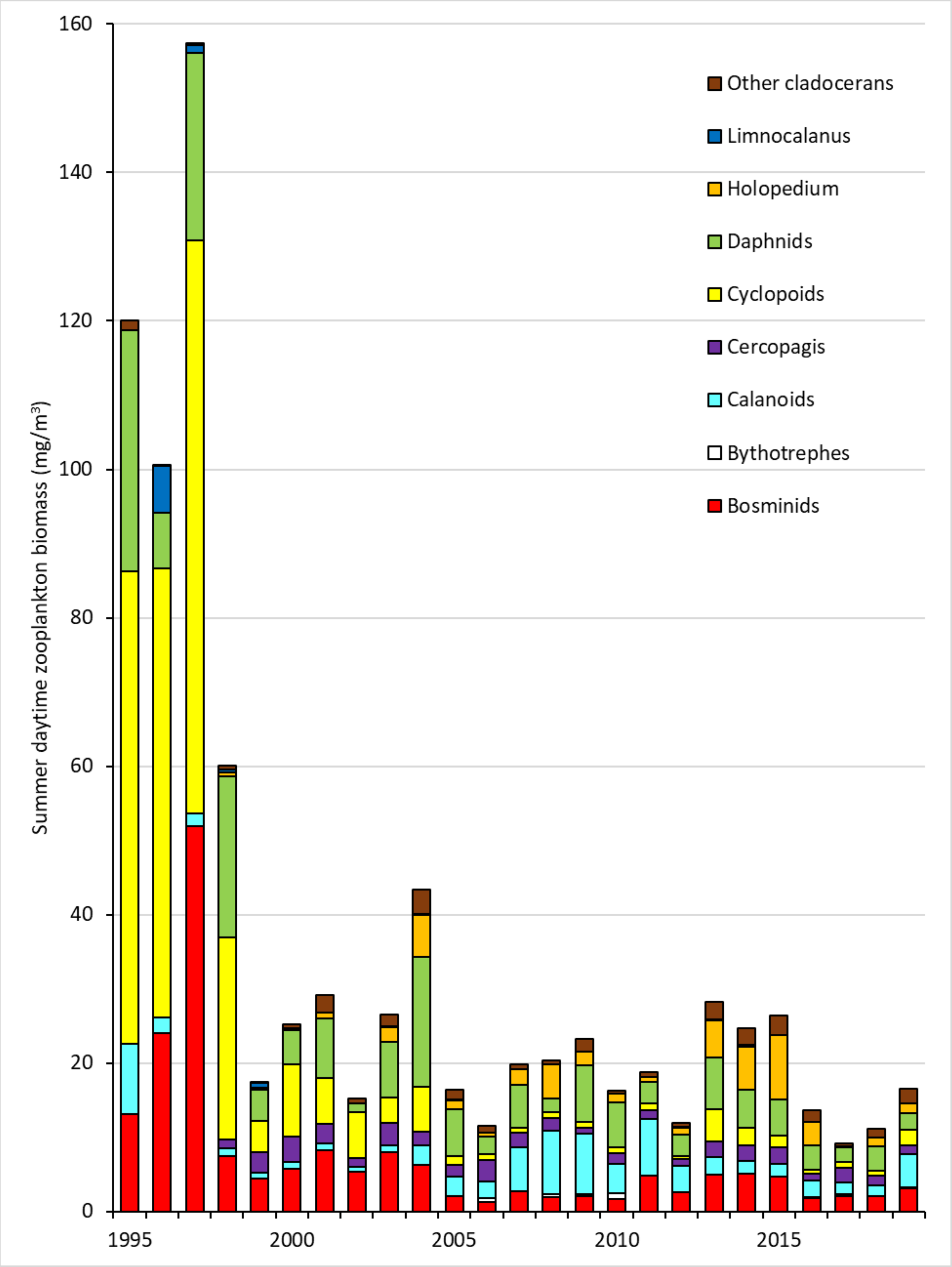


Figure 11. Mean summer (Jul – Aug) daytime nearshore zooplankton group dry biomass in Lake Ontario, 1995 – 2019.

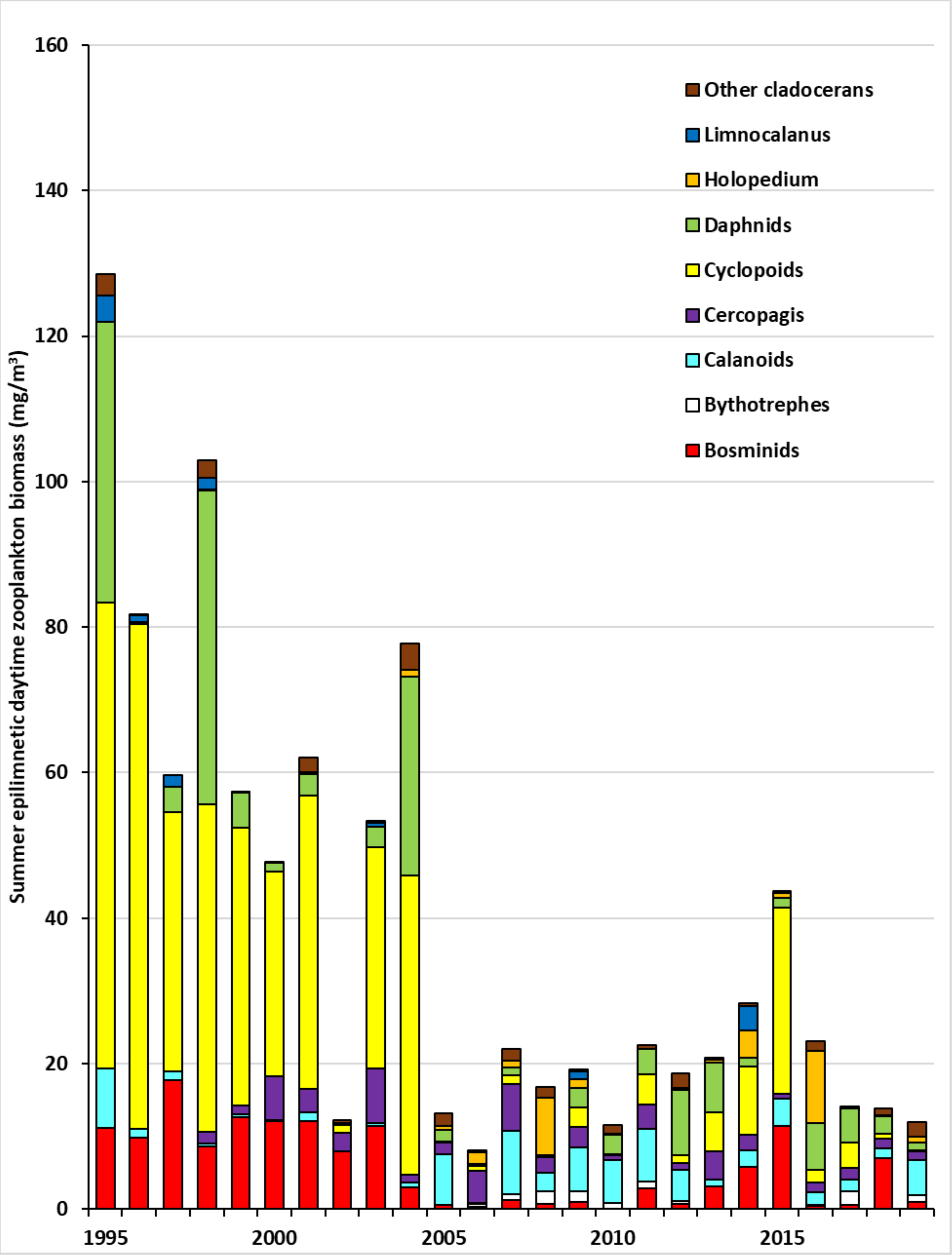


Figure 12. Mean summer (Jul – Aug) daytime epilimnetic offshore zooplankton group dry biomass in Lake Ontario, 2000 – 2019.

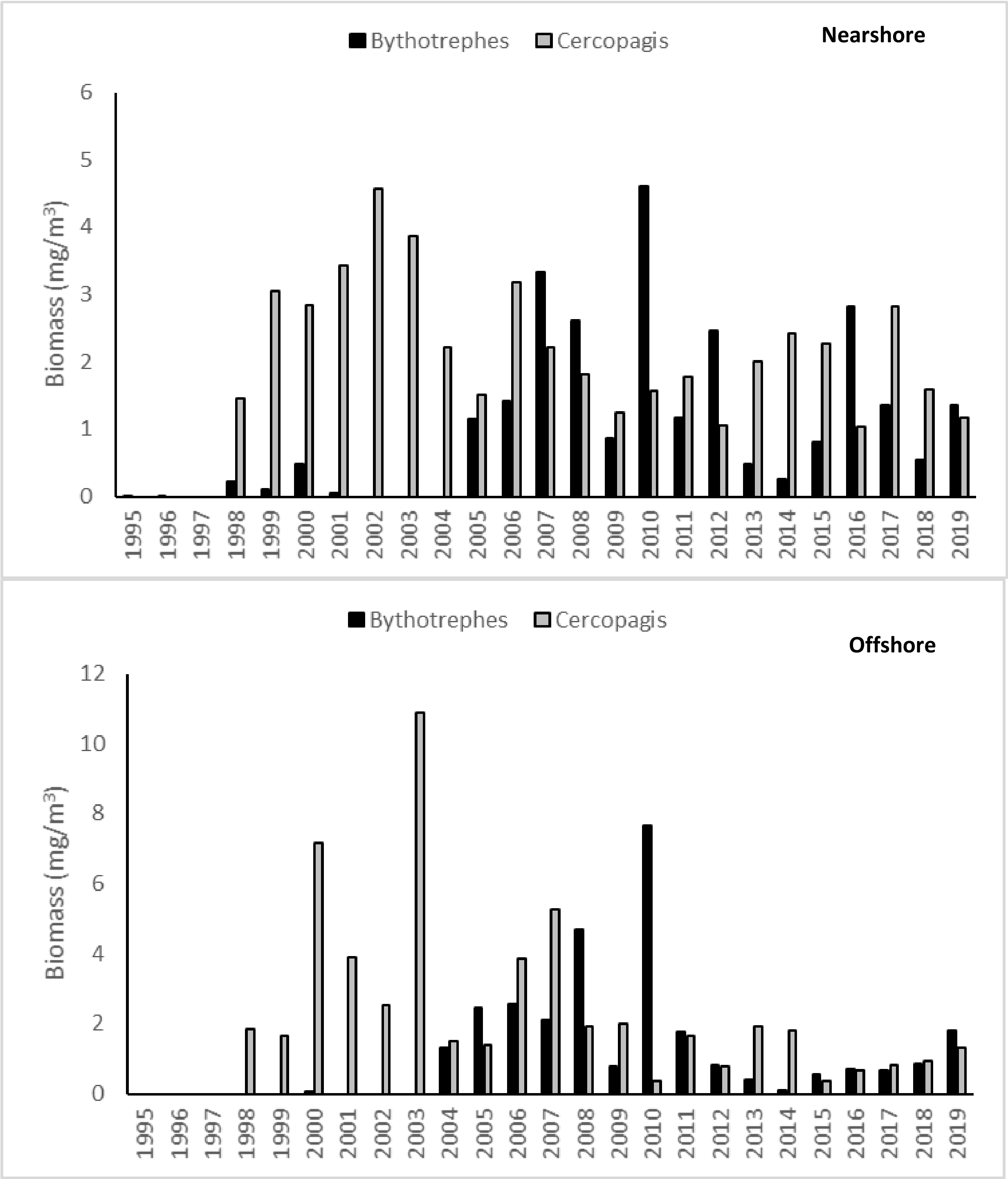


Figure 13. Daytime epilimnetic nearshore and offshore fall (September and October) **Bythotrephes** ***and summer (July and August)*** **Cercopagis** ***dry biomass in Lake Ontario, 1995 – 2019. Months were selected based on timing of peak biomass for each species.***

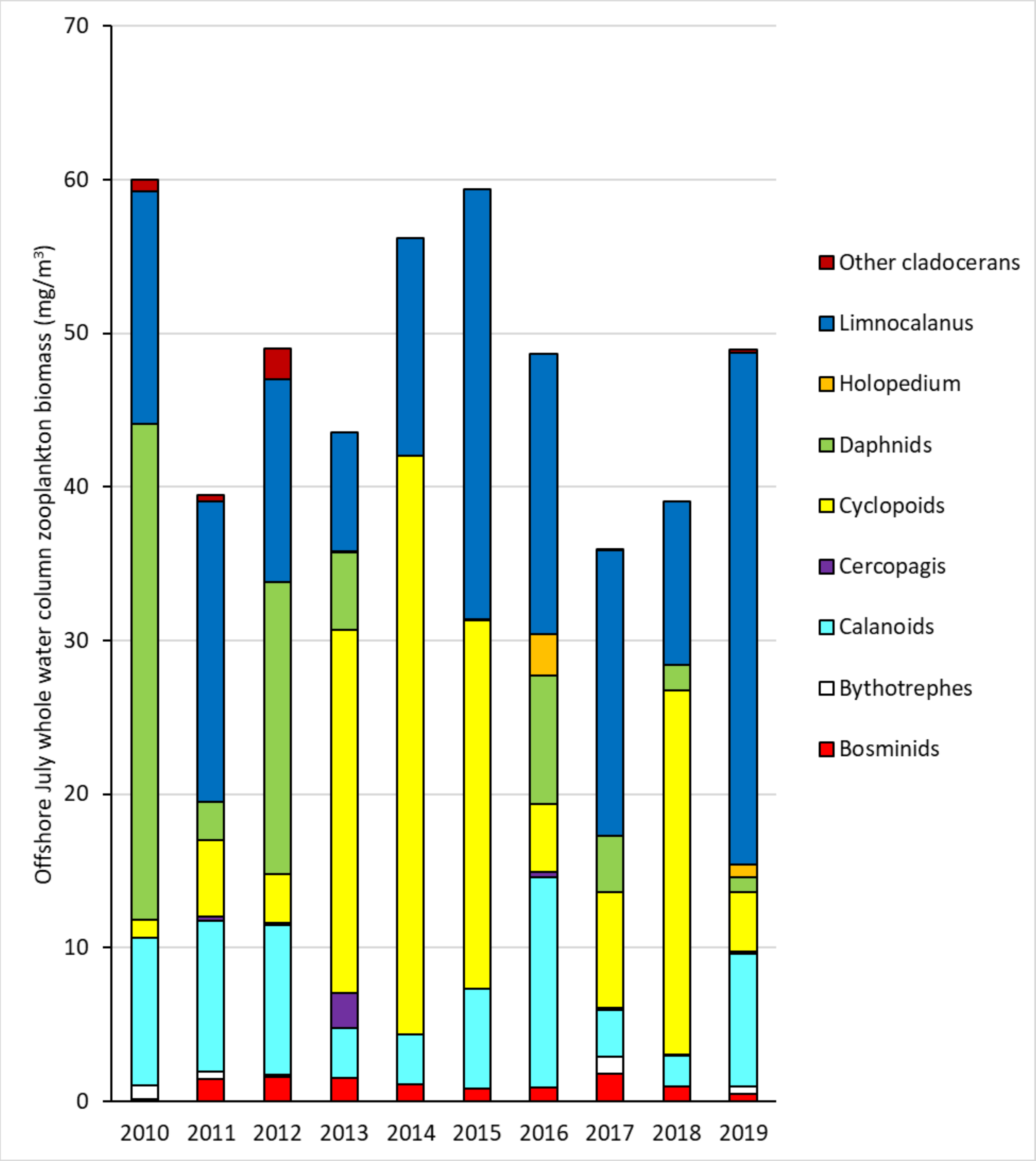


***Figure 14.* Mean July whole water column offshore zooplankton group dry biomass in Lake Ontario, 2010 – 2019.**

Table 1. Mean chl a, TP, SRP and Secchi depth (± 1 SE) for nearshore and offshore sites, April – October 2019.

	Mean ± 1 SE			
Sites	Chlorophyll-*a* (µg/L)	Total phosphorus (µg/L)	Soluble reactive phosphorus (µg/L)	Secchi depth (m)
Nearshore				
Chaumont Lake (CBL)	2.9± 0.4 (n=12)	6.5± 0.9 (n=12)	1.1± 0.2 (n=12)	5.2± 0.6 (n=12)
Galloo Island (GIL)	1.6± 0.2 (n=12)	5.9± 1.2 (n=12)	0.8± 0.1 (n=12)	7.7± 0.4 (n=12)
Oak Orchard (OOL)	1.7± 0.2 (n=12)	4.5± 0.4 (n=13)	0.6± 0.01 (n=13)	6.1± 0.4 (n=13)
Sodus Lake (SOL)	1.6± 0.2 (n=11)	4.5± 0.4 (n=11)	1.0± 0.2 (n=11)	7.3± 0.8 (n=11)
Sandy Pond Lake (SPL)	2.6± 0.4 (n=8)	5.0± 0.8 (n=8)	0.7± 0.1 (n=8)	5.0± 0.6 (n=7)
Niagara East Lake (NEL)	1.8± 0.1 (n=12)	5.1± 0.6 (n=13)	0.6± 0.01 (n=13)	4.1± 0.4 (n=13)
Niagara West Lake (NWL)	1.2± 0.2 (n=13)	5.3± 0.5 (n=12)	0.7± 0.1 (n=13)	3.8± 0.4 (n=13)
Offshore				
Kaho				
Oak Orchard-N	1.8± 0.5 (n=4)	5.0± 0.6 (n=4)	0.9± 0.2 (n=4)	7.9± 2.6 (n=4)
Oak Orchard-O	2.0± 0.8 (n=4)	5.0± 1.5 (n=4)	0.7± 0.04 (n=4)	8.4± 3.2 (n=4)
Smoky Point-N	1.6± 0.4 (n=4)	4.3± 0.6 (n=4)	1.1± 0.3 (n=4)	8.1± 1.8 (n=4)
Smoky Point-O	1.9± 0.5 (n=4)	4.1± 0.7 (n=4)	0.8± 0.1 (n=4)	6.0± 1.6 (n=4)
Seth Green				
Main Duck	1.5± 0.2 (n=3)	3.7± 0.3 (n=3)	0.8± 0.2 (n=3)	8.2± 1.3 (n=3)
Mid Lake	1.3± 0.6 (n=3)	4.3± 0.9 (n=3)	0.8± 0.2 (n=3)	9.1± 2.1 (n=3)
Tibbetts Point	1.9± 0.3 (n=3)	4.1± 1.5 (n=3)	0.7± 0.03 (n=3)	8.1± 0.6 (n=3)

Table 2. Comparison of nearshore and offshore sites Apr/May-October, 2019 by fitting a mixed effects model with month and habitat as fixed effects and site as a random effect on log-transformed (TP, SD, chl-a, zooplankton size, density and biomass) or untransformed (SRP, zooplankton group biomasses) Apr/May – Oct mean values. SRP and zooplankton group biomass could not be normalized and the Wilcoxon test was used for those comparisons. Reported p-values are for the significance of habitat, not month. Values shown are arithmetic means summarized by site and then across months 4/5, 7, 9, and 10. Months 6 and 8 were removed from the analysis because the offshore was not sampled during those months. All offshore data are for the epilimnion (zooplankton) or the top 10 m (water chemistry).

		Mean		
Parameter		Nearshore	Offshore	p-value
	Total phosphorus (µg/L)	5.2	4.6	0.07
	Soluble reactive phosphorus (µg/L)	0.8	0.8	0.9
	Chlorophyll *a* (µg/L)	1.7	1.8	0.6
	Secchi depth (m)	5.7	7.6	**0.05**
Total zooplankton:				
	Density (#/m^3)	8605	7559	0.2
	Size (mm)	0.61	0.72	**0.02**
	Biomass (mg dw/m^3)	23.7	25.0	0.7
Group biomass (mg dw/m^3):				
	Bosminids	2.3	2.3	1.0
	Daphnids	6.0	5.8	0.9
	Calanoid copepods (excluding *Limnocalanus*)	8.9	9.3	0.7
	Cyclopoid copepods	3.8	3.2	0.3
	Other cladocerans (excluding *Holopedium*)	0.3	0.6	0.2
	Cercopagis pengoi	0.4	0.4	1.0
	Bythotrephes longimanus	0.4	1.1	0.4
	Holopedium gibberum	0.9	1.2	0.9
	Limnocalanus macrurus	0.3	1.0	0.9

Table 3. Results of regression analyses performed on data from three time stanzas (1995 – 2019, 1995 – 2004, and 2005 – 2019) in Lake Ontario's offshore and nearshore. TP data were available from 2002 – 2019 in the offshore. Trends are indicated by (+) or (-). Significant p-values (p=<0.05) are indicated in bold. Marginal p-values (p<0.10) are indicated in italics. ns=not significant. nd=no data. Slope is from the linear regression and represents the annual change in each parameter (units of change match the units of each parameter). Zooplankton group biomass could not be normalized; Spearman rank correlation was used on those data, but change reported is the slope of the linear regression. Change point analyses were performed on 1995 – 2019 in the both the offshore and nearshore. **change point performed on ranks due to outliers.

	Regression						Change Point Analysis
Offshore	1995 – 2019	Slope	1995 - 2004	Slope	2005 – 2019	Slope	1995 - 2019
Spring TP (µg/L) (2002 – 2019)	ns		nd		ns		no breaks
Summer Secchi Depth (m)	**(+) p=0.016**	**0.1**	**(+) p=0.01**	**0.3**	ns		no breaks
Summer chlorophyll *a* (µg/L)	**(-) p=0.007**	**0.04**	ns		ns		(-) 2009
Summer epilimnetic zooplankton density (#/L)	**(-) p=0.0007**	**1692**	**(-) p=0.03**	**3192**	ns		(-) 2005
Summer epilimnetic zooplankton biomass (µg/L)	**(-) p=0.0002**	**3.2**	ns		ns		(-) 2002
Summer epilimnetic zooplankton group biomass (µg/L)							
Bosminids	**(-) p=0.0025**	**0.4**	ns		ns		(-) 2004
Bythotrephes longimanus	**(+) p=0.0135**	**0.03**	ns		ns		no breaks
Calanoid copepods	ns		ns		ns		no breaks
Cercopagis pengoi	ns		**(+) p=0.03**	**0.5**	ns		(+) 2000
Cyclopoid copepods	**(-) p=0.0007**	**2.2**	ns		ns		(-) 2005, (+) 2013
Daphnids	ns		ns		ns		no breaks
Other Cladocerans	ns		ns		ns		no breaks
Limnocalanus	***(-) p=0.0509***	**0.04**	**(-) p=0.008**	**0.3**	ns		no breaks
Holopedium	**(+) p=0.0079**	**0.1**	**(+) p=0.016**	**0.06**	ns		no breaks

	Regression						Change Point Analysis
Nearshore	1995 - 2019	Slope	1995 - 2004	Slope	2005 – 2019	Slope	1995 -2019
Spring TP (µg/L)	ns		ns		ns		no breaks
Summer Secchi Depth (m)	ns		**(+) p=0.0012**	**0.13**	ns		no breaks
Summer chlorophyll *a* (µg/L)	ns		**(+) p=0.0033**	**0.12**	ns		(-) 2009
Summer epilimnetic zooplankton density (#/L)	**(-) p<0.0001**	**1902**	**(-) p=0.0192**	**6528**	ns		(-) 1998
Summer epilimnetic zooplankton biomass (µg/L)	**(-) p=0.0001**	**3.2**	**(-) p=0.0209**	**12.2**	ns		(-) 1998
Summer epilimnetic zooplankton group biomass (µg/L)							
Bosminids	**(-) p=0.0008**	**0.7**	ns		ns		**(-) 2005
Bythotrephes longimanus	**(+) p=0.0087**	**0.005**	ns		ns		(+) 2006, (-) 2011
Calanoid copepods	ns		ns		ns		(+) 2007, (-) 2012
Cercopagis pengoi	ns		**(+) p=0.0302**	**0.3**	ns		no breaks
Cyclopoid copepods	**(-) p<0.0001**	**2.0**	**(-) p=0.0038**	**8.1**	ns		(-) 2005
Daphnids	**(-) p=0.0031**	**0.7**	ns		ns		no breaks
Other Cladocerans	**(+) p=0.048**	**0.04**	**(-) p=.0289**	**0.2**	ns		no breaks
Limnocalanus	ns		ns		ns		**no breaks
Holopedium	**(+) p=0.0021**	**0.1**	**(+) p=0.0046**	**0.4**	ns		(+) 2003